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Spruce Beetle in the Rockies

J. M. Schmid and R. H. Frye

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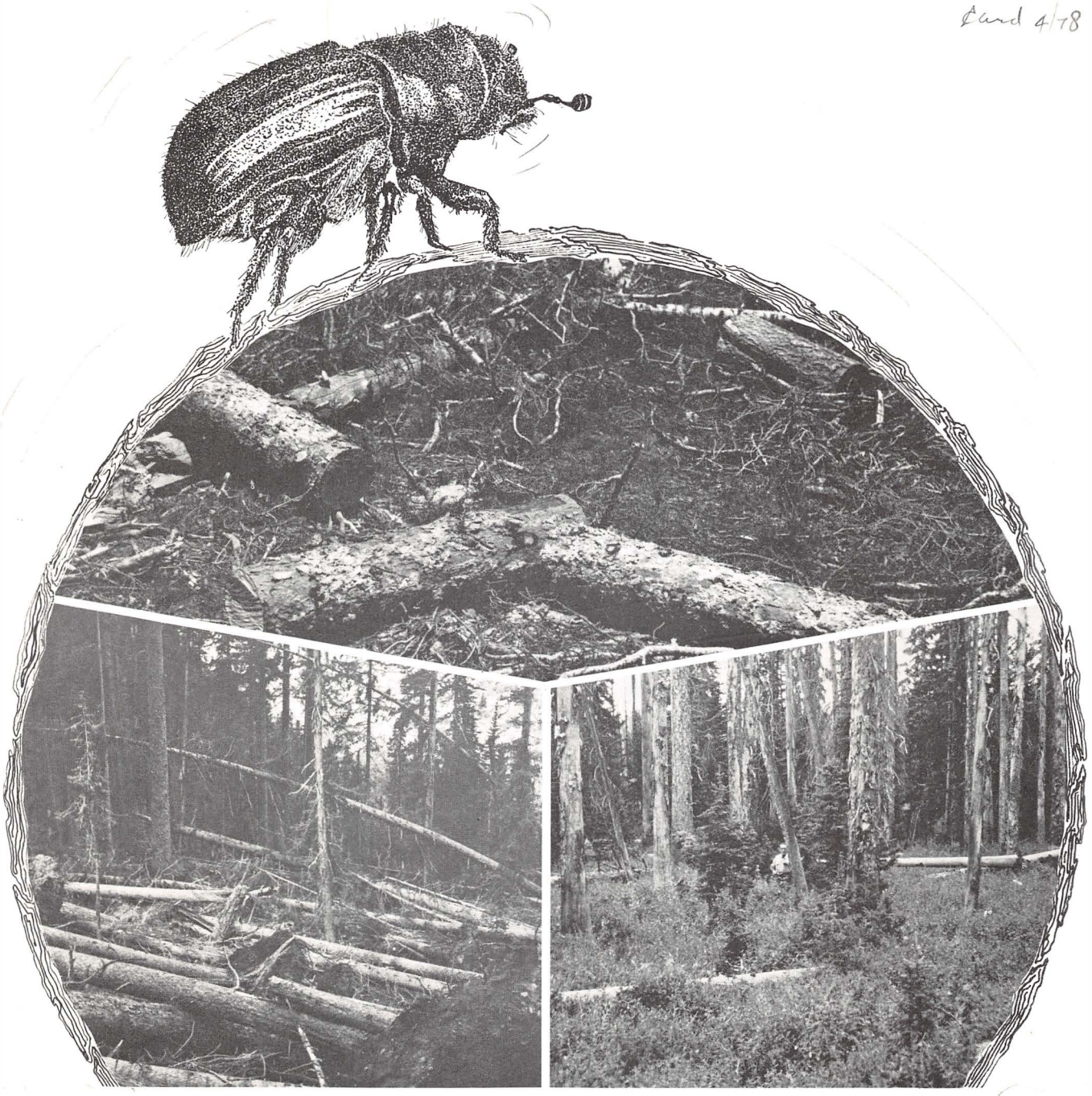

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Abstract

This report summarizes the literature on the spruce beetle in the western United States, primarily in the Rocky Mountains. Information is presented on life history and behavior, host relationships, mortality agents and impacts of infestations. A section on suppression details the current status of chemicals, pheromones, trap trees and silvicultural treatments. The initial steps in managing spruce beetle populations are stated in the final section on beetle management policy.

Although this report discusses research involving pesticides, such research does not imply that the pesticide has been registered or recommended for the use studied. Registration is necessary before any pesticide can be recommended. If not handled or applied properly, pesticides can be injurious to humans, domestic animals, desirable plants, fish, and wildlife. Always **read** and **follow** the directions on the pesticide container.

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and

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Dedication

This paper is dedicated to Dr. Noel Wygant, one of the pioneers in spruce beetle research. Dr. Wygant's knowledge of the White River outbreak and the spruce beetle in general has been generously shared with those of us who followed his early work and pursued spruce beetle research. We consider ourselves privileged to know him.

[1]Central headquarters is maintained at Fort Collins in cooperation with Colorado State University.

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Spruce Beetle in the Rockies

J. M. Schmid and R. H. Frye

Preface

This report summarizes the available literature on the spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera:Scolytidae), in western North America. While it is primarily concerned with the beetle in the central and southern Rockies, recent work in the northern Rockies and Alaska is also reviewed. However, the information in the report is most applicable to the Rockies and British Columbia, not Alaska.

The literature from the Rockies is mostly derived from research projects in Colorado where spruce beetle research has received increased emphasis since the White River outbreak in the 1940's. Generally, survey reports, biological evaluations, and other unpublished material are not cited except for those that contain a particularly significant finding. Where information was lacking for subjects such as insect predators or impacts on a watershed, it has been derived from other studies. Observations and opinions of the authors have been expressed in certain sections.

The primary purpose of this report is to assemble pertinent information under common binding so that foresters can easily find answers to their questions.

Taxonomy

Before 1963, six species of *Dendroctonus* beetles inhabiting spruce were recognized in North America. The best known spruce beetle in the western United States was *D. engelmanni,* the *Dendroctonus* beetle originally described by Hopkins (1909a) from Engelmann spruce in New Mexico. In 1963, Wood synonymized *D. engelmanni* with *D. rufipennis* (Kirby), *D. similis* LeConte, *D. piceaperda* Hopkins, *D. borealis* Hopkins, and *D. obesus* (Mannerheim). He presented *D. obesus* as the senior name, and thus designated a single species inhabiting a broad geographical area and several species of spruce. However, *D. rufipennis* was an older name which had priority. Wood corrected this oversight in 1969, thereby establishing *D. rufipennis* (Kirby) as the proper name.

These recent name changes have created some confusion among foresters in the central Rockies. Publications referring to *D. engelmanni* prior to 1963 and to *D. obesus* from 1963 to 1969 are relevant for them. From 1969 to the present, articles and reports concerned with *D. rufipennis* are pertinent.

Previous Outbreaks

The tree killing potential of the spruce beetle has been well documented during the last 100 years. On the White River National Forest, Colorado, in the mid-1870's, 10%-25% of the mature spruce were found dead (Sudworth 1900a); while 25%-40% of the mature spruce on the Grand Mesa, Colorado were also dead (Sudworth 1900b). Hopkins (1909b) later confirmed the spruce beetle as the cause of this mortality. These early estimates of the mortality may be slightly exaggerated because they are based on random surveys on horseback. Three years before these Colorado outbreaks, Hopkins reported 90% of the spruce mortality on more than 13,000 acres (5,261 ha) in the White Mountains of the Lincoln National Forest, New Mexico, was attributable to spruce beetles. Between 1916 and 1918, an infestation began on the Aquarius Plateau, Utah, that eventually killed nearly all the large spruce before it subsided in 1928-29 (Mielke 1950).

More recently, the Grand Mesa and White River National Forests, Colorado, have had extensive outbreaks. An infestation in the 1940's killed more than 50% of the merchantable volume of spruce on the Grand Mesa (Struble 1944*)[2]. Simultaneously, the most damaging outbreak in recorded history decimated spruce stands on the White River National Forest (Massey and Wygant 1954). There, the amount of tree mortality was so incredible that a precise estimate of the volume of dead spruce is unavailable, although 3.8 billion board feet (fbm) (23 million m^3) is commonly quoted.

In the last 15 years, an extensive outbreak in British Columbia killed more than 3 billion fbm (18.2 million

[2]*References followed by an asterisk are listed in the unpublished references section.*

m^3), while further north around the Cook Inlet, Alaska, beetles have caused tree mortality on more than 420,000 acres (169,680 ha) (Schmid and Beckwith 1975). At the other extreme of the spruce beetles' range, beetles killed more than 50,000 trees in the White Mountains of the Fort Apache Indian Reservation, Arizona, from 1968 to 1971; more than 15,000 trees on the Santa Fe National Forest, New Mexico, from 1968 to 1971; other, less serious, infestations occurred in Arizona and New Mexico (Lessard 1976). Smaller outbreaks in the early 1970's near Wolf Creek Pass, Colorado and Encampment, Wyo., killed hundreds of spruce (Schmid 1971b). These outbreaks caused the death of many especially large trees near creek bottoms (fig. 1). Other outbreaks in the 1970's on the San Juan and Gunnison National Forests in Colorado and on the Medicine Bow National Forest in Wyoming have caused similar amounts of damage.

Annual mortality attributable to spruce beetles is difficult to determine because, except for outbreaks, much of the mortality originates from single or small groups of trees scattered throughout forests. Wood (1963) estimates one-third to one-half billion fbm (2 to 3 million m^3) are lost annually; the Timber Resources Review (U. S. Department of Agriculture 1958) estimated the 1952 loss at 552 million fbm.

All known major outbreaks have originated from stand disturbances such as blowdown, cull, or right-of-way logging operations (Wygant and Lejeune 1967). Widely scattered blowdown is especially conducive to increases in beetle populations (Wygant and Lejeune 1967) and is a prime source of outbreaks. Over a 3-year period in British Columbia, windfall averaged 1-2 trees per ha on 766 ha (Dyer and Safranyik 1977), so this material would be more than adequate to maintain a population. Logging operations have also started outbreaks (McCambridge and Knight 1972). Where one million fbm (6,061 m^3) or more of mature spruce is harvested for more than three successive years, spruce beetle problems will occur (Hester 1960*), but these may not always develop to outbreak proportions. Problems can originate when much less than one million fbm is cut (Baker 1977*).

Beetle numbers during outbreaks are seldom quantified. One observation during the White River outbreak staggers the imagination but epitomizes the millions of beetles that characterize this incredible outbreak. According to Wygant (1950*), Dr. Lee Yeager observed, in July 1949, a layer of beetles 6 inches (15 cm) deep and 6 feet (1.8 m) or more wide along the eastern shore of Trapper's Lake on the White River National Forest, Colorado (the eastern shore is more than 1 mile (1.6 km) long.

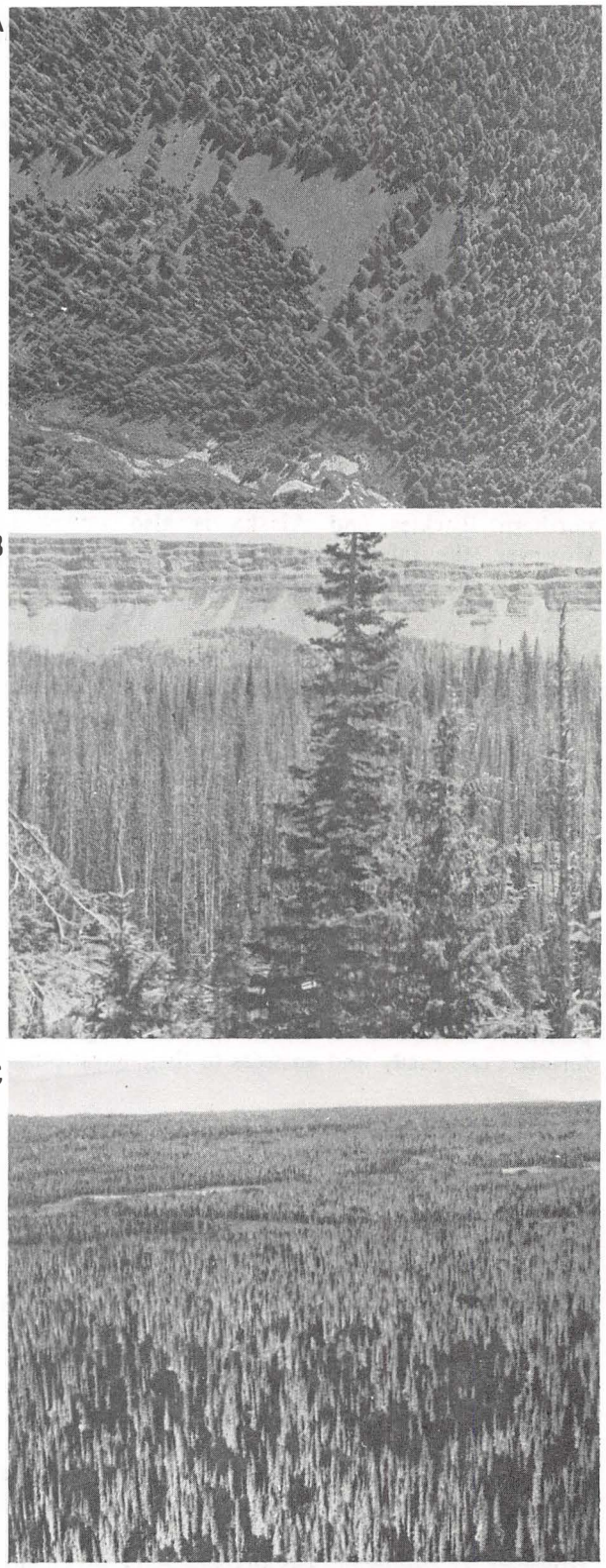

Figure 1.—Extensive tree mortality on the (A) San Juan National Forest, Colorado; (B) White River National Forest, Colorado; (C) land near Tyonek, Alaska.

Hosts

The spruce beetle infests all species of *Picea* in North America. In the southern and central Rockies, Engelmann spruce (*Picea engelmannii* Parry) is the principal host, while blue spruce (*P. pungens* Engelmann) is an infrequent host. White spruce (*P. glauca* (Moench) Voss) and Sitka spruce (*P. sitchensis* (Bongard) Carr) are the principal hosts in Canada and Alaska.

Under outbreak conditions, lodgepole pine (*Pinus contorta* Douglas) has been killed by the spruce beetle during the White River outbreak (Massey and Wygant 1954), and spruce beetles attacked 140 lodgepole pine in north central Colorado in 1957 but did not kill the trees nor produce brood (McCambridge and Knight 1972). Wood (1963) notes that the lodgepole pine beetle (*D. murrayanae* Hopkins) superficially similar to the spruce beetle, caused much of the lodgepole pine mortality attributed to the spruce beetle in the White River outbreak. He has been unable to confirm any of the reports that the spruce beetle was responsible for this mortality (Wood 1977*). However, Massey (1975*) personally examined many infested lodgepole pine, and definitely attributes the mortality to the spruce beetle.

The attack of lodgepole pine by the spruce beetle may be another example of a *Dendroctonus* beetle attacking an atypical host under outbreak conditions when the atypical host is mixed with the common host. The mountain pine beetle (*Dendroctonus ponderosae* Hopkins), a species usually attacking trees in the genus *Pinus,* has attacked white spruce in the Black Hills where individual spruce trees have been occasionally mixed with the predominant host, ponderosa pine (*Pinus ponderosa* Lawson) (Schmid 1965*). Thus, it seems highly probable that other species of *Dendroctonus,* such as the spruce beetle, could attack atypical hosts like lodgepole pine when they are mixed with Engelmann spruce.

Engelmann spruce is widely distributed throughout western North America and is usually found between 9,000-11,000 feet (2,700-3,353 m) elevation in the central Rocky Mountains (U. S. Department of Agriculture 1965). It grows in the coldest and highest forest environment in the Rockies in the United States, characterized by annual temperature extremes of below -40° F (-40° C) in winter and over 80° F (26.7° C) in summer. Annual precipitation exceeds 25 inches (63.5 cm), most of which falls as snow.

Subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) is a common associate at all elevations in the central Rockies and comprises a variable percentage of the canopy. Lodgepole pine and quaking aspen (*Populus tremuloides* Michaux) are less common associates. Blue spruce is an associate along creek bottoms at lower elevations.

Spruce sawtimber (Engelmann and blue spruce) on commercial forest land in Colorado was estimated to be about 25 billion fbm (152 million m^3) in 1959 (Miller and Choate 1964). Similarly, the volume in New Mexico was estimated to be 3.3 billion fbm (20.1 million m^3) in 1962 (Choate 1966). In 1970, the net volume of Engelmann and blue spruce sawtimber on commercial timberlands was estimated to be 22.3 and 2.7 billion fbm (136 and 16 million m^3) in Colorado and New Mexico respectively (U.S. Department of Agriculture 1973). In 1975, 29 billion fbm (177 million m^3) of sawtimber existed on National Forest lands in Colorado (Cahill 1976*). This sawtimber exists on 2.5 million acres (1,010,000 ha), of which 75% or 1.9 million acres (768,000 ha) is in either a roadless or "reserved" (wilderness, natural area, etc.) category.

The amount of spruce sawtimber cut in Colorado was 106, 131, and 130 million fbm (646,799, and 793 thousand m^3) in fiscal years 1966, 1967, and 1968 respectively (Bailey 1969*). More recently, the volume of Engelmann spruce sawtimber cut in Colorado and Wyoming was 90.7, 98.0, and 60.8 million fbm (553, 598, and 371 thousand m^3) in fiscal year 1973, 1974, and 1975 respectively (Lister 1976*).

Life History and Behavior

Description of Stages

The following descriptions are mostly from Hopkins (1909a), Massey and Wygant (1954), and Wood (1963). More detailed descriptions are also available from these sources.

Egg - oblong, pearly white, 0.75-1 mm in length.

Larva - a white, stout, cylindrical, legless grub, 6-7 mm in length at maturity. Four instars in the larval stage,

Pupa - creamy white, similar in size to the adult.

Adult - dark brown to black with reddish brown elytra; older adults uniformly black. The initial coloration of the adult after transformation from the pupae is white. The adult gradually darkens and thus is white, light brown, and dark brown before becoming mostly black. Adults in the white-to-brown color phase are commonly called callow adults. Length is 4.4-7 mm. Average weight of 50 adults from Green Mountain near Encampment, Wyo., was 16.8 mg. (Schmid 1972*). The compound eye of a spruce beetle contains an average of 272 ommatidia (Chapman 1972).

Life Cycle

The 2-year life cycle as described by Massey and Wygant (1954) is generally common to endemic and outbreak infestations (Knight 1961), although a 1-, 3-, and perhaps 4-year cycle is possible. In the 2-year cycle, adults usually attack in June and July. By mid-October, nearly all of the eggs have hatched and the larvae have developed to the second, possibly fourth, instar. The larvae overwinter, diapausing during the winter before resuming development in the spring. This probably has survival value in very cold climates when severe cold might kill the pupae (Dyer 1970). Sometime during late spring-early summer (about 1 year after attack) the larvae pupate, then transform into adults. The second winter is passed in the adult stage and the following summer they emerge to attack host material.

Beetles can develop from the egg to the adult in less than 1 year when they are inhabiting host material on mountain slopes in a temperature inversion region below 5,000 feet (1,524 m) above sea level in southeastern British Columbia (Dyer 1969). Such slopes commonly develop higher minimum temperatures which accelerate the development during the immature stages. Dyer (1969) assumed the adults would be ready to attack after their 1-year cycle, but he did not follow the adults the next year to determine if this was true.

On warmer sites at lower elevations in the southern and central Rockies, spruce beetles may complete their life cycle in one year, overwintering as new adults and attacking the following summer (Massey and Wygant 1954). In this part of the Rockies, natural stands of Engelmann spruce do not exist at elevations below 8,000 feet (2,438 m), but the more southern latitude may make conditions similar to those Dyer studied. However, it is doubtful if a high proportion of any beetle population in Colorado completes its development and attacks host material within 1 year.

The 3-year cycle is less frequent than the 2-year cycle but more frequent than the 1-year cycle. Massey and Wygant (1954) and Wygant (1959) suggested the 3-year cycle, while Knight (1961) and McCambridge and Knight (1972) documented the conditions contributing to delayed maturation. On a north facing slope in north central Colorado, rate of development was slowed by cold summer weather so that 50% of the beetles in standing trees emerged after 3 years of development and 40% to 57% in felled trees emerged after 3 years (Knight 1961). Similar results were obtained by McCambridge and Knight (1972) in another infestation. In both instances, however, trees were partially infested in successive years; thus the degree of certainty of the 3-year cycle is questionable.

The 4-year cycle, also proposed by McCambridge and Knight (1972), is possible but not yet supported by definitive evidence.

As a general rule, the forest manager should use the 2-year life cycle in management decisions.

Emergence

Emergence of adults has three phases: (1) emergence for hibernation, (2) emergence for attack and construction of egg galleries, and (3) reemergence of parent adults after making an initial attack. The latter two may occur simultaneously.

A varying percentage of adults emerge in August and September for hibernation (see the section on hibernation). These beetles exit their place of development in the phloem on the bole of standing trees and move to the base of the tree where they reenter and overwinter. This behavior apparently helps adults survive since egg galleries are not constructed. From 3% to 88% of the beetles may emerge for hibernation (Knight 1961). Fewer than 50% emerged in 1945, whereas 88% emerged in 1954 (Knight 1961). Beetles in downed material do not emerge for hibernation (McCambridge and Knight 1972).

Emergence for attack and construction of egg galleries usually occurs in June and July in the southern Rockies, but may begin in May. For three consecutive years (1958-1960), emergence began between June 5 and June 20, continued through June and July, and was nearly completed by the end of July (McCambridge and Knight 1972). In British Columbia, flight began in late May (Dyer 1973). In Alaska, beetles emerged in May and June, with peak numbers flying in late May (Beckwith 1972, Beckwith et al. 1977). Since flight does not occur before the maximum temperature in the shade exceeds the approximate flight threshold temperature (about 61°F or 16°C) (Dyer 1973), this explains why emergence varies annually. If air temperatures in the shade exceed the threshold in May, then emergence takes place. However, in the southern Rockies, this normally occurs in June. Both hibernating adults and adults overwintering in place emerge during this period. Adults usually attack host material within a few days after emerging.

Adults emerge and attack host material and then may emerge a second time. The number of reemerging adults is not equally divided between the sexes; males tend to leave earlier and more of them reemerge (Wood 1977*). The number of reemerging adults approached 100% in standing trees (Massey and Wygant 1954)

although only about 20% immediately began a second gallery. In British Columbia, reemergence from pheromone-baited trees was 16% in mid-July, another 18% by early August, and the last 51% between mid-August and mid-September (Lawko and Dyer 1974). However, these trees were pheromone-baited and may not have been attacked under normal conditions; therefore, reemergence may have been abnormal. Furthermore, the percentages represent the percentage of females that reemerged, not the total population. That percentage would be considerably less.

Wood (1977*) notes that many factors appear to influence this habit. It may have been influenced by the severity of resin flow (Lawko and Dyer 1974). Other authorities have speculated that the density of attacks or egg galleries influences the females and causes some to reemerge.

There has also been speculation that this behavior may be a possible explanation for the rapid increase in spruce beetle populations. That is, females could construct a gallery with a complement of eggs, then reemerge, move to another host tree and repeat gallery construction and egg deposition. Each female would thus be constructing two galleries and egg complements so that the population would double, other factors being equal. Data is lacking on whether the reemerging females have completed galleries and laid a full complement of eggs. Data from Lawko and Dyer (1974) suggest that this hypothesis has low probability because, although 18% of the females emerging in late July could fly, the flight muscle in more than 82% of the reemerging beetles had degenerated, making them unable to fly to a new host tree.

Attack Period

Trees may be attacked in May through early August, but if the attack period begins in May, it does not extend into the late summer. In Colorado, attacks began in late June one year and in early July during two other years (Massey and Wygant 1954). Attacks terminated during those years in late July and early August, respectively. McCambridge and Knight (1972) presented an emergence period from early June to late July for three consecutive years which would mean the attack period lasted from early June to early August, depending on the year. Thus, for a specific site, the attack period probably lasts 5 to 6 weeks.

When the attack periods from different sites are considered as one, the attack period may last 3 to 4 months. In exposed logs on the windward side of a small logged area on a south-facing slope in southern Wyoming, attacks were in progress in late May (Schmid 1974*). Approximately 0.75 mile (1.2 km) north of this location, snow depths on a level site in a mature stand exceeded 6 feet (1.8 m) in late May, so beetles did not attack until early July. The difference in the beginning of the attack period is also indirectly substantiated by Chansler (1960) who notes that beetles in a valley flew before those from a site uphill. Since beetle flight and, therefore, attack is dependent on the flight threshold temperature, the duration of the attack period probably reflects the attainment of this threshold under different stand conditions.

Density of Attacks

The density of attacks follows definite patterns depending on the type of host material attacked (standing trees, windthrown trees, trap trees, or logging residuals).

In standing trees, attack densities decrease with increasing height (table 1). The mean number at any specific height differs between infestations, but ranges within definite limits. Attacks have not exceeded a mean value of 10 per square foot (929 cm^2) at breast height where many trees were sampled. Attack densities on the largest diameter trees were not significantly greater than on the smallest diameter trees in aggregation tests in British Columbia (Dyer 1973).

The number of beetles required to successfully attack a standing tree varies with the density of attacks and the bark surface area of the tree. The bark surface area is mainly determined by the diameter and height of the tree. If attacks are held constant in the various

Table 1.—Mean number of attacks per square foot (929 cm^2) of bark surface on standing trees by height.

Massey and Wygant 1954		Knight 1960a		Frye et al. 1977	
Height	Mean	Height	Mean	Height	Mean
1-15	8	0-5	6.6	5	4.2
16-30	5	5-10	5.6	15	2.1
30+	Decreasing	10-15	4.7	25	1.9
		15-20	4.3	35	0.6
		20-25	3.5	45	0
		25-30	3.1		
		30-35	2.7		

zones of the bole, then trees of smaller diameter (7-8 inches or 17-20 cm) at breast height (d.b.h.) receive fewer attacks because of their smaller diameter and short height. In trees 7-14 inches (17-36 cm) d.b.h., the number of beetles absorbed increases primarily because of increases in height. Total attacks on trees greater than 14 inches d.b.h. increase primarily because of increases in tree diameter. Since beetle attacks terminate 40-50 feet (12-15 m) above ground on standing trees, the additional height of these larger trees does not absorb more beetles. When different attack densities are superimposed on different tree sizes, the number of beetles absorbed can show substantial range (table 2).

Two types of unsuccessfully attacked standing trees are infrequently observed in beetle infested areas—pitchouts and strip attacks. Pitchout usually refers to a single unsuccessful beetle attack surrounded by a mass of white pitch. Forest entomologists have broadened its definition to also include those trees exhibiting a large number of pitched-out attacks which have apparently survived the mass attack of the beetles. This has led to some confusion because the word has been used for both meanings without specific definition during its usage. For this report, pitchout and strip attack are defined as follows.

The pitchout is a tree that survives attack densities apparently lethal to other trees. Such trees usually exhibit masses of pitch around the entrance holes to the galleries. The galleries are extremely short, rarely extending more than 1 inch (2.5 cm) in the phloem, and brood is not produced. Pitchouts are rare, observed in fewer than one out of 100 attacked trees.

The strip attack is a tree that sustains attacks on only one side, usually less than one-half the circumference. The number of attacks making up the strip is quite variable, and brood production therein is usually poor. Such trees are more frequently observed than the pitchout and are usually seen on the periphery of a large group of attacked trees or quite distant from other attacked trees when the infestation is somewhat irregular and scattered in the stand.

Strip attacked trees reflect the number of beetles in the attacking population or perhaps a decreasing population. As the attack period ends, only a small number of beetles are left to infest material. If the previously attacked trees are filled with attacks, these beetles must attack uninfested green trees, but there are not enough to attain a uniform density around the circumference. Thus, they attack one side, usually that side that faces the group of infested trees.

Neither pitchout nor strip attack trees die after the attacks. The pitchout does not develop blue stain because the attacks do not penetrate deeply enough or the resinous galleries are unsuitable for fungal growth. The strip attack may develop blue stain in the successful zone of the attack, but the rest of the tree remains unaffected. Pitchouts and strip attacks frequently die in subsequent years because they are infested again by another generation of spruce beetles or other scolytids.

Table 2.—Mean numbers of attacks and beetles to cause mortality in a standing tree of specific d.b.h., based on attack densities from Frye et al. 1977, and Knight 1960a.

D.B.H. (inches)	Frye et al. 1977 Number		Knight 1960a. Number	
	Attacks	Beetles	Attacks	Beetles
7	67	135	111	222
8	97	195	159	317
9	140	280	226	452
10	171	342	282	564
11	204	409	343	685
12	232	463	399	798
13	259	518	463	925
14	276	553	495	989
15	303	607	541	1,082
16	317	635	568	1,135
17	334	669	600	1,199
18	366	732	660	1,319
19	392	784	711	1,422
20	412	823	745	1,489
21	431	862	780	1,559
22	458	916	831	1,662
23	484	968	880	1,760
24	506	1,013	921	1,842
25	530	1,060	965	1,929

In windthrown trees, trap trees, and logging residuals except stumps, attack densities are generally highest on the bottom surface, intermediate on the lateral surfaces, and lowest on the top (tables 3, 4, and 5). The lateral surfaces may have densities greater or equal to those on the bottom surface if the bottom has been damaged or is in contact with the ground. Generally, shading increases the attack density on all surfaces (table 4). Attacks on the upper surface are very scarce (approaching zero) where the bark surface is exposed to the sun. In some cases, *Ips* beetles may attack prior to the spruce beetle and completely occupy the upper surface. Attack densities may also approach zero on the bottom surface if that surface is in contact with the ground.

Table 3.—Low and high mean number of attacks per square foot (929 cm²) of bark surface in windthrown trees.

Surface	Low	High	Range
Top	0.3[a]	0.9[a]	0.6
Lateral	0.7[a]	5.1[a]	4.4
Bottom	1.5[a]	5.9[a]	4.4
All Surfaces	0.8[b]	4.2[b]	3.4

[a] *J. M. Schmid, Unpublished data.*
[b] *Dyer and Taylor 1971*

Table 4.—Mean numbers of attacks per square foot (929 cm²) of bark surface on trap trees. Data from Buffam, Buffam et al., and Lister et al. for the check trees in Silvisar experiments.

Surface	McComb 1953				Nagel et al. 1957		Buffam 1971		Buffam et al. 1973		Lister et al. 1976
	Sunlight		Shaded		Full Sun	Dense Shade	Frilled	No Frill	Ariz.	Colo.	
	Low	High	Low	High							
Top	1.5	8.2	7.0	16.5	1.9	8.7					
Lateral	12.9	17.3	17.6	23.4	11.1	17.8					
Bottom	12.7	16.5	16.0	26.7	12.7	18.4	12.1	9.6	2.6	7.6	6.2

Table 5.—Low and high mean numbers of attacks per square foot (929 cm²) of bark surface on logging residuals.

Dyer and Taylor 1971			Schmid 1977		
Stumps	Mean		Stumps	Mean	
	Low	High		Low	High
Top-shaded	0.9	3.5	Top	2.9	9.3
Bottom-shaded	2.3	5.6	Bottom	2.0	5.4
Logs			**Logs-8'+**		
Top-sun	0.0	0.2	Top	0.3	1.6
Bottom-off ground	0.2	1.0	Lateral	0.5	4.4
Bottom-on ground	2.2	4.5	Bottom	1.2	8.7
			Tops		
			Top	0.4	1.2
			Bottom	1.0	3.4

Attack densities may vary significantly along the length of the bole for any particular surface. McComb (1953) found that attacks varied little along the boles of trap trees, but Schmid (1977) found significant differences in the attack densities within any of the three surfaces of cull logs exceeding 8 feet (2.4 m). Differences along the top surface of exposed material are caused by unequal exposure or shading. Along the bottom surface, densities are significantly different due to ground contact or, in cut logs, dehydration of the inner bark adjacent to the cut surface.

Bark scale length, scale exfoliation (degree of separation from the bark) and bark thickness did not influence attack density on trap trees (Jennings 1959*). However, Jennings found attacks present in bark that ranged in thickness from 0.1 to 0.25 inches (2.5 to 6.4 mm) which may explain why attacks are rare in the extremeties of the bole on downed material.

Attack densities may differ significantly between individual windthrown trees or pieces of logging residual. This also develops because of unequal shading and the size of the attacking population. Unequal shading is frequently caused by the type of windthrow—complete or sporadic toppling of the trees within the stand—or by the logging procedures—felling trees into the uncut forest and piling cull logs or tops.

Attack density is also influenced by the attacking population. Lister et al. (1976) noted that, when the population is large and the number of trap trees (or windthrown trees or logging residuals) is small, the density of attacks is considerably higher than when the opposite conditions exist. Attack densities may also be less variable within and between the infested materials.

Some forest entomologists have hypothesized that some of the variation in attack densities reflects secondary attacks by females. Generally, females probably attack only once. They may create two galleries if they are disturbed during initial gallery construction in the first gallery. They will very rarely attack a tree, construct a gallery and lay a complement of eggs, then emerge and repeat the sequence on another tree. As noted earlier, Lawko and Dyer (1974) showed that more than 80% of the reemerging beetles were unable to fly and thus, could not fly to another tree to begin another gallery. However, there is the possibility that a reemerging female could crawl along the surface of the tree she originally attacked and create a second gallery somewhere else on the tree. While this is a greater possibility, it is also unlikely. The probability that either type of secondary gallery construction could initiate an outbreak is remote.

Egg Galleries and Eggs

Females construct the egg gallery in the phloem with a slight grooving of the xylem (Massey and Wygant 1954). The initial portion of the gallery has a slight crook, but, thereafter, is almost straight and extends upward in standing trees. In downed material, galleries usually extend parallel to the bole. Ventilation holes, when present, are constructed at irregular intervals along the gallery (Wood 1963). As the gallery lengthens, more of the initial portion is packed with frass. Egg galleries in trees injected with silvicides are frequently short, "U", "S", or "Y" shaped (fig. 2) and void of packed frass (Frye and Wygant 1971).

The length of individual galleries varies. Mean length of 218 examined galleries was 5 inches (12.7 cm), while the maximum and minimum were 9 inches (22.9 cm) and 2.5 inches (6.4 cm) respectively (Massey and Wygant 1954). In Utah, average length was 5 inches (13 cm) and maximum length was 9 inches (23 cm) (Wood 1963). Mean gallery length in silvicide injected trees was 1.9 inches (4.8 cm) versus 4.3 inches (10.9 cm) for the untreated trees (Frye and Wygant 1971).

Eggs are deposited in different ways; usually in individual niches or elongate grooves placed on alternate sides of the gallery. Some galleries may have all the eggs in separate niches (Wood 1963). Massey and Wygant (1954) reported eggs were deposited in alternate groups; two to five groups per gallery was common.

The number of eggs per gallery varies. Massey and Wygant (1954) found a maximum number of 144 for 6.1 inches (15.5 cm) of gallery. Average numbers per inch (2.5 cm) of gallery were: 20.5 in standing trees during the White River outbreak (Massey and Wygant 1954), 18.1 in standing trees on the Uncompahgre National Forest, Colorado, and 8.5-9.7 in trap trees on Owl Mountain, Colorado (Knight 1961). Based on these infestations, Knight (1969) proposed that the number of eggs was directly correlated with the stage of the infestation—endemic, epidemic, and declining epidemic infestations producing about 9, 18, and 12 eggs per inch (2.5 cm) of gallery, respectively.

Knight's hypothesis warrants further investigation because Wood (1963) notes that, while the deposition rate in a small infestation in Utah equalled Massey and Wygant's figure of 20.5 eggs per inch (2.5 cm), the rate was maintained only for about one-third the length of the gallery and was confined to the egg deposition area. As the gallery lengthened more of it was unused for deposition, so, the rate decreased. Inspection of the table in Knight (1969) indicates that the mean gallery length was longest where the number of eggs was

A

B

Figure 2.—Egg galleries from (A) natural tree, (B) tree injected with Silvisar 510 prior to attack.

lowest, which supports Wood's statement. Also, it is unclear from Knight's article whether all the data come from standing trees or some may have come from trap trees. The deposition rate in trap trees may be quite different from that in standing trees, thus significantly influencing Knight's hypothesis.

The egg production of nematode infested females may be reduced 40%-70% depending on the species of nematode (Massey 1960*). Nematodes could be a major factor associated with the egg production differences as proposed by Knight (1969).

Egg deposition usually begins less than 1 week after attack, and the eggs incubate 3-4 weeks before hatching (Wood 1963).

Hibernation

Emergence and reentry for hibernation is an idiosyncrasy of the adult spruce beetle in the genus *Dendroctonus*. This behavior is usually exhibited by adults that have not emerged and constructed egg galleries, but Dyer (1973) also found some parent adults hibernating. The habit was first determined by G. R. Struble in 1944 on the Grand Mesa National Forest, Colorado (Massey and Wygant 1954). In the 2-year life cycle in standing trees, a varying percentage of adults emerge during July-September of the second year of development and move to the base of the tree from which they emerged. There each reenters the phloem area by creating its own entrance hole or entering one previously constructed by another adult.

The number or proportion of adults that hibernate varies from year to year; more than 50% may hibernate in some years. Knight (1961) reported as few as 3% and as high as 88% of the adults hibernated on different sites during different years. Densities in the hibernation niche may exceed 300 per square foot (929 cm^2) with more than 10 adults using the same entrance hole (Massey and Wygant 1954).

Spruce beetles do not emerge from trap trees to hibernate (McCambridge and Knight 1972). Based on this finding, it seems improbable that adults would emerge from windthrown trees or logging residuals to hibernate.

Hibernation has a high survival value and may have evolved in response to cold winter temperatures and woodpecker predation. In winter, the basal 6 feet (1.8 m) or more of the bark is covered with snow. The ambient air temperatures above the snowline may be below -40° F (-40° C) (lethal to the beetle) while below the snowline, temperatures are near 32° F (0°C). The snow cover also prohibits woodpeckers from feeding on the brood below the snowline. The combined effect of these factors is higher beetle mortality in the above snowline population. Thus, any beetle leaving the upper bole and hibernating in the basal section has a greater chance of surviving.

Dispersal

Beetles can fly long distances. Flight mill tests indicate a few beetles can fly more than 7 miles (11.3 km) nonstop (Chansler 1960, Shaw 1961). Under field conditions, flight distances may exceed 15 miles (24 km), but it is not known if flight is maintained continuously. As the White River outbreak began to terminate in the Flat Tops country, beetles dispersed from there to near Rabbit Ears Pass, Colorado, a distance of more than 15 miles (24 km) over non-host habitat (Wygant 1976*). Beetles also flew 30 miles (48 km) south from the Flat Tops to establish new infestations south of the Colorado River (Nelson 1954, Wygant 1956, Wygant 1959). While these beetles may have been aided by strong winds aloft, they could have flown a major portion of this distance.

Beetles fly when the air temperature exceeds the flight threshold temperature of about 61° F (16°C) (Dyer 1973). This would account for early beetle activity in open-logged areas where air temperatures are warmer, while emergence and flight occurs later in dense stands.

Beetle populations exhibit considerable variation in flight ability, number of flights, duration of the flight and speed. From 7% to 29% of the population did not fly in flight mill tests (Chansler 1960). Of those that did, 33% were extremely poor fliers (Chansler 1960). Some beetles flew more than 10 times, but 78% flew three times or less. Those beetles that flew three or fewer times, flew for 12-17 minutes during each flight. Those that flew 10 times or more, flew 6 minutes during each flight (Chansler 1960). Some beetles flew continuously for 35 minutes or more. During these flights, the flight speed was high initially, decreased during the first 10 to 20 minutes, and then became constant thereafter (Chansler 1960). Initial speeds averaged 256 feet (78 m) per minute. The presence of internal nematodes did not appear to influence the ability to fly; their effect on speed and endurance could not be determined (Chansler 1960).

The size of the lateralis medius muscle can be used to judge the flight capability (Gray and Dyer 1972). When the average median index of the muscle is within a range of .14-.175 mm, female beetles are capable of flight. Using this index, Lawko and Dyer (1974) found that 82% of the beetles reemerging at certain periods after attacking host material were unable to fly. Those

emerging after August 1 could not disperse to attack additional host material.

Slightly more beetles disperse in an easterly direction than in a westerly direction (Schmid 1970c). This is probably caused by predominantly westerly winds in the spruce-fir country. However, beetles could generally move in one specific direction against predominant winds if an attraction source existed in that direction.

More beetles were recovered at trap trees within one-quarter of a mile, or 20 chains (0.4 km) of the release point than from 1 mile, or 80 chains (1.6 km) (Schmid 1970c). This also indicates that beetles can fly longer distances but will fly only short distances if suitable host material is available.

Under field conditions, the natural dispersal period of the population probably takes place over several weeks, although individual beetles are searching for host material for only several days. Radioactively tagged beetles (Davis and Nagel 1956) dispersed for about 1 week after release (Schmid 1970c). The greatest number of attacks were made 3-5 days after beetle release (Schmid 1970c), which indicates that the majority of the beetles searched and found suitable host material within this period.

Mortality during dispersal is unknown. Passerine birds consume an undetermined percentage of the adults either on the bark or in flight (Baldwin 1969). In studies of the mountain pine beetle in ponderosa pine, birds consumed up to 8.5% (Stallcup 1963). Some forest entomologists believe adult mortality during dispersal may exceed 50%. In view of the low recovery rate (3%-4%) of released beetles derived in dispersal studies (Schmid 1970c), mortality may well exceed that value.

Considerable research effort is needed on dispersal mortality because future tree mortality predictions and trap tree programs are based on estimates of numbers of attacking beetles. We know that the numbers of attacking beetles will be less than the brood estimates derived from our latest samples but we don't know how much less. Thus, our predictions of the number of infested trees or trap trees will be more precise when dispersal mortality is better known.

Sound Production

Sound is produced by both sexes of the spruce beetle. Females produce an infrequent "spontaneous" click by rubbing a sternal file of ridges against a file of ridges along the sutural margin and tip of the left elytron (Rudinsky and Michael 1973). Sounds from gallery constructing females may have an intraspecific

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Susceptibility

Susceptibility of standing trees is difficult to define. We can define what trees are more likely to be attacked, but the trees may be attacked because they are more conducive to beetle survival rather than more susceptible. Any standing tree can be killed if enough beetles attack it naturally, but, as noted earlier, large numbers of beetles do not always attack each tree. Nearly all trees naturally subjected to attack densities of 4-6 per square foot (929 cm^2) at breast height, and decreasing vertically thereafter but present to a height of at least 30 feet (9 m), will die. With only strip attacks, or fewer than four attacks per square foot (929 cm^2) at breast height for 10 feet (3 m) or less of the bole, most trees will survive.

The spruce beetle prefers certain host material which may or may not relate to susceptibility. It prefers downed material to standing trees, and the size of the downed tree is less important than the exposure of its bark to sunlight or contact of the bark with the ground. If downed material is unavailable, then standing trees may be attacked. Large diameter standing trees (>20 inches or >51 cm d.b.h.) are preferred to small diameter trees, (6-8 inches or 15-20 cm d.b.h.), but larger trees are preferable if they are relatively free of live branches in the basal section and grow in a competitive stand where natural pruning occurs rather than in an open grown situation without competition and with live limbs in the basal portion.

Susceptibility can be recognized more easily and precisely in stands than in individual standing trees. Knight et al. (1956) outlined the order of susceptibility of spruce stands as follows:

1) Spruce in creek bottoms
2) Better stands of spruce on benches and high ridges
3) Poorer stands on benches and high ridges
4) Mixtures of spruce and lodgepole pine
5) Stands containing all immature spruce

Unmanaged stands can be rated for their susceptibility to potential outbreaks by using the average diameter of the spruce, basal area, species composition and physiographic location (Schmid and Frye 1976). Within these four characteristics, three levels of risk are recognized. Potentially high risk stands usually have an average diameter at breast height over 16 inches (41 cm); basal area of more than 150 square feet per acre (14 m^2 per 0.4 ha); and more than 65% spruce in the canopy and located in a well-drained creek bottom. Low risk stands usually have: an average diameter of less than 12 inches (30 cm); basal area of less than 100 square feet per acre (9 m^2 per 0.4 ha); less than 50% spruce in the canopy; a site index of 40 to 80.

The question frequently arises, "How long is windthrown spruce suitable for beetle infestation?" Unpublished data taken in Rocky Mountain National Park, Colorado, and the Jemez Mountains, Sante Fe National Forest, New Mexico, by Schmid, indicate that windthrow can remain attractive through two attack periods. If a tree remains unattacked during the first possible attack period, then it may be attacked during the second possible attack period, about 1 year later, providing it doesn't unduly desiccate. If it is partially or completely infested during the first possible attack period, then additional infestation is unlikely 1 year later.

Windthrown spruce varies in the duration of its suitability because the windthrow may be the upper portions of trees that have been broken off from the lower bole, or trees partially or totally uprooted. Partially uprooted trees have some root contact with the soil and remain green even though they lie horizontally. Broken off trees and totally uprooted trees lose contact with the soil and die soon after falling. They probably desiccate and become unsuitable faster than partially uprooted trees.

Logging residuals differ from windthrown trees in that the trees have been dismembered and more exposed to direct sunlight. Unless substantially shaded, logging residuals are probably suitable for infestation only during the first possible attack period; thereafter, infestation is unlikely. During the first possible attack period, *Ips* may invade the host material, especially along the top surface, and contribute to the drying process.

Characteristics of Infested Trees

Newly infested standing trees can be distinguished from noninfested trees in a stand by the presence of reddish-brown boring dust in the bark crevices and around the base of the tree—characteristics visible from 10 feet (3 m) or more depending on the amount of frass accumulation. Small, 0.1-inch (.25 cm) frass-clogged entrance holes and occasional open, "ventilation" holes may be visible in the bark. Masses of pitch accumulating around the entrance holes, commonly called pitch tubes, are rare at eye level but are more prevalent on the upper bole where the attacks terminate. The needles on infested trees remain the same color as those on uninfested trees, and few drop during the first summer and fall (Schmid 1976). Needle temperatures of infested trees are the same as those of uninfested trees (Schmid 1976). From an aerial viewpoint, newly infested trees can not be differentiated from uninfested trees during the summer of attack.

Windthrow or logging residuals will not generally show accumulations of frass beneath the tree nor pitch tubes on the bark, but do show frass in the bark on the bottom surfaces.

During the winter months following the summer of attack, woodpecker activity is a good sign of infested trees. Partially debarked trees and accumulations of bark chips around the base can be seen from more than 100 feet (30 m) away, especially against the background of snow, whether on the ground or from the air (fig. 3). The debarked condition and accumulations of bark chips are also visible in succeeding months, but the bark chips on the ground are less noticeable after the snow melts unless the trees are heavily woodpeckered.

Approximately 1 year after beetle attack, clusters of needles die and discolor, turning yellowish-green in the process. Massey and Wygant (1954) reported that the needles on most trees turn this yellowish-green color and fall about one year after attack. More recent evidence suggests that about 30% of the needles on a tree discolor and fall during the summer, which is about 1 year after attack (Schmid 1976). These are the older needles, furthest from the tips of the branches. At the same time, the infested trees may add new growth so that the tips of the branches appear similar to uninfested trees. This partially camouflages the discolored needles and prevents easy aerial detection. Needles that die and discolor do not remain on the tree for months, as do needles from beetle-infested pines, but frequently are removed by winds and rain. Boring dust is less noticeable during this second summer due to dissipation, weathering and coverage by other debris.

As the trees approach the third summer (about 2 years after attack), most of the needles will have discolored making the infested tree appear yellowish-green. The previous loss of needles exposes more branches, giving the tree a grayer appearance. Sometime during this summer, storms strip the remaining needles, and the tree appears as a gray skeleton (Schmid 1976).

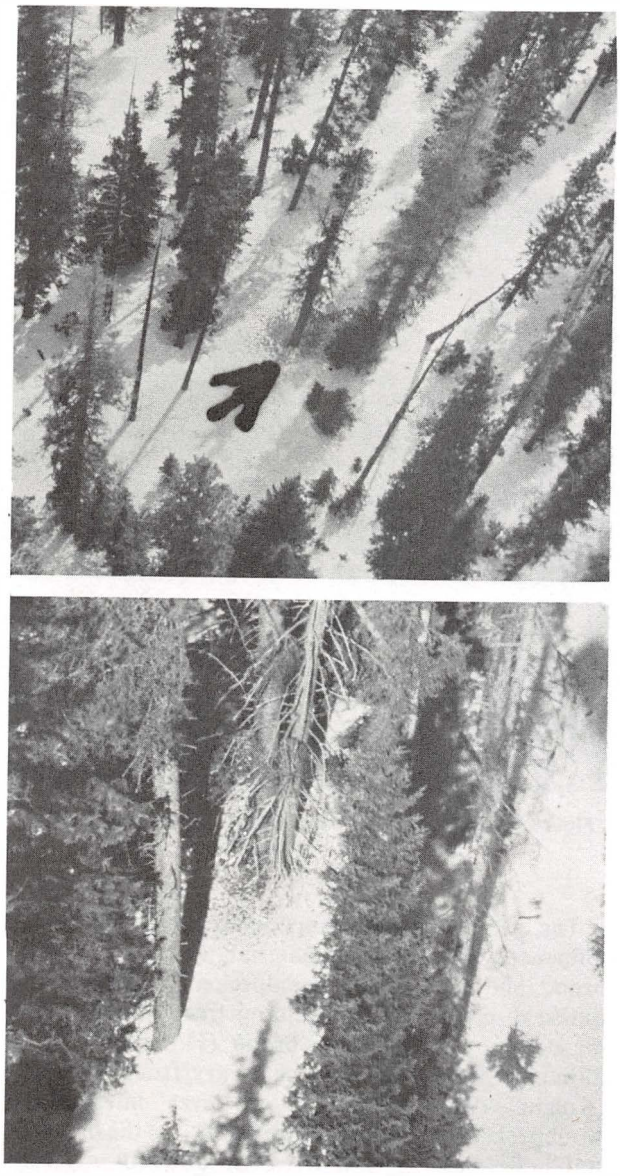

Figure 3.—Infested trees may be more noticeable from the air in winter because the bark accumulates around the bases of trees debarked by woodpeckers. Bark around the base of the tree is almost a sure sign the tree is infested by spruce beetles.

Blue Staining Fungi

The spruce beetle transports several species of fungi which develop in the trees the beetle infests (see the section on Deterioration). Some of these fungi impart a blue-gray color to the sapwood (outer xylem), commonly called blue stain. *Leptographium engelmannii* Davidson is the most prominent species consistently associated with the spruce beetle in Engelmann spruce (Davidson 1955). This species was the most common blue stain fungus in trap trees in New Mexico (Hinds and Buffam 1971). *Ceratocystis trunicola* (Davidson) is frequently present in the egg galleries (Davidson 1955). Hinds and Buffam (1971) found *C. olivacea* (Mathiesen) Hunt, and *C. coerulescens* (Munch) Bakshi, in fewer than 10% of their test trees.

Blue stains can completely penetrate the sapwood within a year (Hinds and Buffam 1971). During their development, they occlude the outer conducting tissues in the xylem and essentially stop translocation. This action, plus the destruction of the phloem by the beetles, kills the tree.

The development of blue stain fungi is inhibited in Engelmann spruce by Silvisar 510 (Frye and Wygant 1971). The inhibition is related to dosage—full strength permitted 5% or less of the sapwood volume to be stained, while 30%-35% was stained in the controls when 2 or more weeks elasped between injection and felling (Hinds and Buffam 1971).

Effects of Temperature and Biotic Factors

Temperature

Temperature is one of the most critical factors in the life of the spruce beetle—the extremes are lethal, and the intermediates influence development. Laboratory tests showed that subcortical temperatures of -15° F (-26.1°C) will kill all adults, while -30° F (-34°C) will kill all larvae (Massey and Wygant 1954). Extremely low temperatures in Colorado in 1951 are frequently cited as a major factor in terminating the White River outbreak (Wygant 1956). In the northern Rocky Mountains, an average of 42% of the brood was killed during a cold spell (Terrell 1954). Frye et al. (1974) attributed high larval mortality (88%) in the Fort Apache outbreak to -40°C temperatures in January (fig. 4). At the opposite extreme, temperatures exceeding 130° F (54.5°C) for 30 minutes will kill all

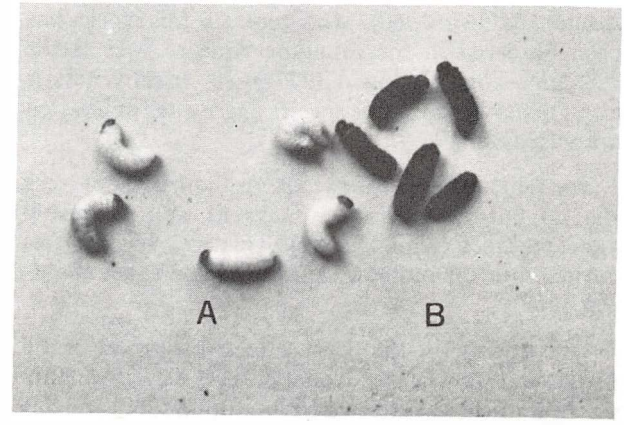

Figure 4.—Below zero temperatures may cause substantial mortality to the larvae; (A) normal larvae, (B) larvae killed by severe cold.

the brood in the bark subjected to such conditions. Temperatures above 110° F (43.5°C) will kill varying percentages of the brood depending on the length of exposure (Mitchell and Schmid 1973).

Temperatures intermediate to these extremes can either accelerate or prolong the normal life cycle. Especially warm temperatures during the summer months (Knight 1961) or temperature inversions on particular slopes (Dyer 1969) can shorten the 2-year life cycle to 1 year. Warmer temperatures cause the larvae to avert diapause and continue development (Dyer 1970). Contrastingly, unusually cold temperatures during the summers can prolong the life cycle to 3 years (Knight 1961, McCambridge and Knight 1972).

The hibernation habit of adults may have evolved in response to cold winter temperatures. When beetles leave the upper bole and reenter the bark near the base, their survival is enhanced because, under normal conditions, 6 feet (1.8 m) or more of snow accumulates on the ground in winter in the spruce-fir forest and covers the bases of the trees. Below this snow line temperatures are near 32° F (0°C), while above the snow line ambient air temperatures exist. Thus, beetles in the bark below the snow line are not subjected to lethal sub-freezing temperatures.

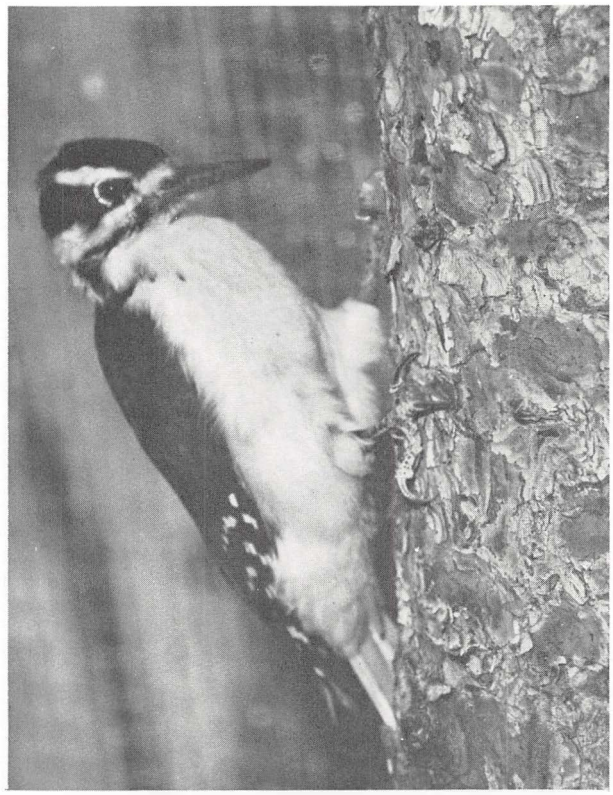

Figure 5.—Woodpeckers are the most important predator.

Woodpeckers

Three species of woodpeckers, the northern three-toed, *Picoides tridactylus* Baird, the hairy, *P. villosus* (Anthony), and the downy, *P. pubescens* (Hartlaub), are important predators of the spruce beetle (Knight 1958) and are listed in decreasing order of importance.

The northern three-toed is most effective because it feeds exclusively on the boles of trees—primarily on trunks of freshly attacked trees rather than old snags (Koplin 1969)—and is indigenous to the spruce-fir habitat (Baldwin 1960). More recently, this species has been observed in the montane zone as well as the subalpine zone (Baldwin 1977*). Its effectiveness is also greater because this species aggregates in infested areas (Koplin 1969).

The hairy woodpecker feeds on the trunks of trees (fig. 5) but examines old snags as well as freshly attacked trees (Koplin 1969). This woodpecker frequents both the montane and subalpine zones (Baldwin 1969).

The downy is the least effective spruce beetle predator of these three woodpeckers. It feeds mainly on the branches of infested trees (Koplin 1969) and has the least pronounced functional response to infestations (Koplin 1972). This species also frequents both the montane and subalpine zones (Baldwin 1969).

The effect of woodpeckers on beetle populations is influenced by the host material, density of beetle brood, and extent of the woodpecker feeding. During outbreak conditions in standing trees, woodpeckers may destroy 55% of the brood (Hutchison 1951), although beetle mortality may vary from 45%-98% (Knight 1958). During low level infestations, woodpeckers may only take about 20% of the brood in standing trees. In trap trees, or downed material, woodpeckers may consume 2%-26% of the brood (Koplin and Baldwin 1970). Although this last citation supports Knight's (1960b) contention that woodpeckers are not effective on beetle populations in downed material, Baldwin (1968) reported a 70%-79% reduction of beetles in windthrown trees. Feeding activity on trap trees or downed material may be influenced by the presence or absence of adjacent, infested, standing trees. When present, feeding activity on the downed material may be reduced. When absent, woodpeckers may concentrate on the downed material.

Feeding activity of woodpeckers fluctuates with the season, day, weather, and infested host material. Feeding on infested standing trees is generally highest during December through March; feeding is greatly reduced on such trees from late May to September

(Koplin and Baldwin 1970). On clear days in winter, feeding begins at daylight, becomes inactive at midday, and resumes in late afternoon (Hutchison 1951, Amman and Baldwin 1960, Baldwin 1960). During winter snowstorms, feeding activity coincides with midday (Hutchison 1951, Amman and Baldwin 1960). In summer, woodpeckers are equally active all day (Koplin 1969). More feeding takes place when the air temperature is below 10° F (-12° C) than when it is above 20° F (-7° C) (Hutchison 1951). In winter, woodpeckers feed predominantly on that part of standing trees above the snow. Snow covering downed trees and the bases of standing trees precludes feeding therein. As the snow recedes in spring, more of the basal section is exposed, but by this time woodpeckers have dispersed. Feeding is commonly limited to seven to eight infested trees until the larvae are no longer available (Hutchison 1951). This creates heavy predation on some trees and relatively light predation on others.

Woodpecker densities per unit area fluctuate with the season and available supply of beetles. During the nesting season, densities may be one pair per 1,000 acres (405 ha) when populations are very low (Baldwin 1969), or six pairs per square mile (259 ha) (Shook and Baldwin 1970), or one pair per 100+ acres (41 ha) in areas of low beetle populations (Baldwin 1968). Peak densities in a vast outbreak (100 square miles or 25,900 ha) appeared to be nine per acre (0.4 ha) (Yeager 1955). This may be the upper limit of woodpecker density during the nesting season because territoriality and antagonistic behavior limits their density.

Woodpecker densities during non-breeding season may reach 30-45 per acre (0.4 ha) when there are numerous infested trees concentrated in a small area (Baldwin 1960). This is due to aggregation through drift, rather than an increase from reproduction (Koplin 1969). At such times, 12 woodpeckers may feed on two adjacent trees (Baldwin 1969).

Beetle larvae may be 99% of the woodpecker's diet in winter but will constitute a lesser amount in summer. Adults (parent and new) may be consumed during winter feeding, but since the larvae are much more numerous, woodpeckers feed mostly on them and rarely confine their feeding exclusively to new adults. Depending on the species, a woodpecker may require at least 1,200-2,200 larvae per day in winter to satisfy its caloric needs when air temperatures are 32° F (0° C) (Koplin 1967). Despite their high energy needs and exclusive feeding on spruce beetles in winter, woodpeckers would be unable to eliminate all the beetles in each tree because some of the beetles hibernate in the base of the tree beneath the protective snow cover. However, woodpeckers indirectly kill some beetles they don't consume by removing the bark and increasing the susceptibility of the beetles to adverse moisture and temperature conditions (fig. 6).

Sapsuckers, *Sphyrapicus thyroideus* (Cassin) and *S. varius* (Linnaeus), and flickers, *Colaptes auratus* (Linnaeus), are associated with beetle infestations (Massey and Wygant 1954, Yeager 1955). They consume mostly vegetable foods and ants (Baldwin 1960) but few spruce beetles. Furthermore, these birds are transients in the spruce-fir forest, present only in summer.

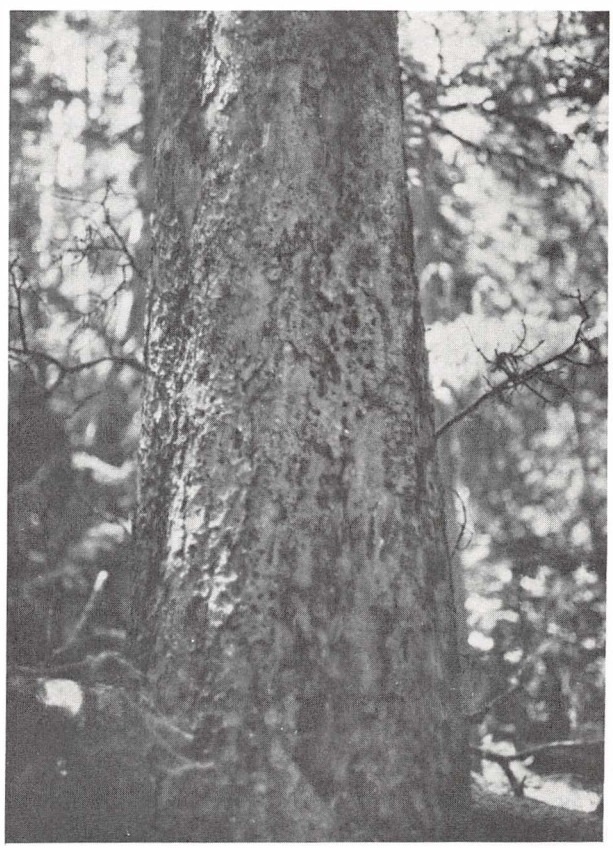

Figure 6.—Woodpeckers debark the infested trees and thus cause substantial mortality as well as providing a means of locating infested trees.

Passerine Birds

The effect of passerine birds (flycatchers, chickadees, etc.) on spruce beetle populations has not been as intensively studied as the woodpecker-beetle relationship. Baldwin (1969) lists the gray-headed junco, *Junco caniceps* (Woodhouse), mountain bluebird, *Sialia currucoides* (Bechstein), and mountain chickadee, *Parus gambeli* Ridgway, as consumers during the flight and dispersal of the beetles. These, plus other less important species, consumed 24%-32%

of the population during one flight period (Baldwin 1969). Passerine birds consumed up to 8.6% of the *D. ponderosae* population during dispersal (Stallcup 1963).

Insect Parasites and Predators

The effects of insect parasites and predators on spruce beetle populations are quite variable. These agents are a tremendous mortality factor in some infestations, perhaps accounting for more than 60% of the beetle deaths. In other cases, the entomophagous species kill a large number of spruce beetles, but their effect on the population is minimal. Some forest entomologists believe insect parasites and predators are primarily responsible for keeping beetle populations at endemic levels. However, the fact remains that infestations develop from a low level to outbreak status with these organisms present. Furthermore, under outbreak conditions, these organisms seldom cause a rapid reduction of the beetle population to preoutbreak levels, even though they may kill a large number of beetles. Based on this, it is difficult to conclude that natural populations of these insect parasites and predators regulate spruce beetle populations.

Generally, the important parasitic and predacious species are known (Massey and Wygant 1954, Jensen 1967). The life cycles, habits, and mortality effects of some species are known either from studies of the spruce beetle or studies on other *Dendroctonus* beetles. Other species are relatively unknown. Some are thought to be predacious or parasitic because they are related to other species that are.

Insect Parasites. *Coeloides dendroctoni* (Cushman) (Hymenoptera:Braconidae) is a solitary parasite with a life cycle of 9-12 months (Ostmark and Knight 1960*). The larval stage externally feeds on the third and fourth instars of the spruce beetle. The female wasp oviposits an egg on or near the larva through the bark (fig. 7). Peak oviposition is in July. The egg hatches in 1 to 4 days. The larval period is very short, less than 1 month in the laboratory. The larva feeds on the host, draining internal fluids and detaching itself when the host larva is almost dry. The parasite commonly spins a white or tan cocoon in which it overwinters. The adult chews through the cocoon and bark; some emerge in late May, but this is probably as variable as spruce beetle emergence. Males usually emerge before females and copulate with them upon their emergence. Adults live 8-15 days in the laboratory without food, slightly longer if supplied a sugary water solution. Females search for host larvae immediately after emergence and seem to prefer late instar larvae. *Coeloides* larvae are not generally found in infested trees until about 1 year after they are attacked. The number of *C. dendroctoni* per square foot (929 cm²) of bark ranged from 0.1 to 2.6. The percentage of brood that is parasitized varied by the status of the infestation—1.7 to 11.3 in static and increasing infestation, 0-60 in decreasing infestations. *Coeloides* is commonly absent in trees that have been heavily woodpeckered.

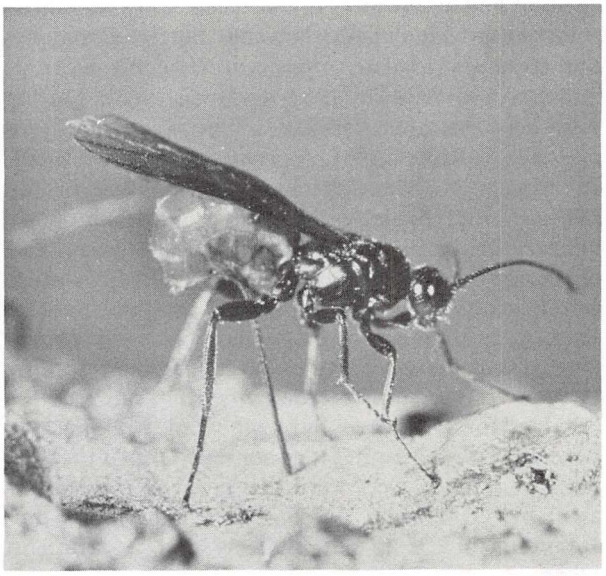

Figure 7. —*Coeloides* **wasp ovipositing in the bark. These wasps are the most important parasites.**

Roptrocerus eccoptogastri Ratzeburg (Hymenoptera:Pteromalidae) adults have been found from May to late August. They are rarely observed in the air or on the bark of infested trees because they are usually within the egg galleries of the spruce beetle, presumably searching for host larvae. No males have been observed, so, the species may be parthenogenetic. In the laboratory, females produced from one to three eggs. Oviposition and eggs have not been observed on beetle larvae, but first instar *R. eccoptogastri* larvae feed externally on the third and fourth instars. They pupate inside the shriveled exoskeleton of the larva and do not form a cocoon. The life cycle is completed in less than 20 days. The numbers of host larvae consumed and densities of the parasite have not been determined.

Cecidostiba burkei Crawford (Hymenoptera: Pteromalidae) is parasitic only on the beetle larvae (Massey and Wygant 1954) but may also be parasitic on insects associated with the spruce beetle. Oviposition habits are thought to be similar to

Coeloides dendroctoni. Adults have been abundant in some locations. Life history and habits of this insect are not well understood.

Insect Predators. *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae) is the second most important biological mortality agent of the beetle; the first is woodpeckers. Its effectiveness may be lessened by indiscriminate feeding habits—larvae feed on the immature states of associated insects (Massey and Wygant 1954). Adults glide over the bark surface, females constantly probing the bark crevices. The eggs are laid in the egg galleries of the spruce beetle (Massey and Wygant 1954). However, on *D. ponderosae* infested trees, *M. aldrichii* eggs were found in degenerate resin ducts (minute depressions) in the bark (Schmid 1970a). The larvae then crawled from these sites to the gallery entrance or another gallery opening to enter (Schmid 1971a). Once in the gallery, the larvae fed on the eggs of *D. ponderosae* and then later on the larvae. *M. aldrichii* pupated in the old phloem. This species accounted for a large portion of the initial mortality to *D. ponderosae,* but its effect on the spruce beetle remains to be determined.

Thanasimus undatulus Say (Coleoptera:Cleridae) adults were active in small numbers in July and August. This clerid is aggregated to living spruce trees by frontalin (Dyer 1973, Dyer 1975) and probably by other pheromones of the spruce beetle. The adults killed a conservatively estimated 3-4% of the adult spruce beetles attacking trees in British Columbia (Dyer et al. 1975). How many spruce beetles they consume in the southern Rockies is unknown. Since they are not abundant, their effect is probably minimal. In Colorado, this species may be primarily predacious on other small scolytids associated with the spruce beetle. Adults consumed an average of one adult *Dendroctonus pseudotsugae* Hopkins per day. Females can produce more than 300 eggs in 7 months in the laboratory (Cowan and Nagel 1965). Eggs hatch in 6-8 days, and the larval stage has three instars. First instar *T. undatulus* larvae feed on first instar spruce beetles. Later instar *T. undatulus* larvae feed on the later larval stages and pupae of the beetle. The larvae apparently overwinter, pupate in spring, and emerge in early summer.

Enoclerus lecontei Wolcott (Coleoptera:Cleridae) adults prey on adult spruce beetles during their emergence and attack period. Adults are active during the summer months. Females lay up to 115 eggs (Cowan and Nagel 1965), probably in the bark. The larvae feed on the larvae and pupae of the spruce beetle. The effect of this species on the adult and larval populations of the beetle is unknown.

Enoclerus sphegeus Fabricius (Coleoptera:Cleridae) adults were most abundant in August and still present in September (Jensen 1967). With other species of *Dendroctonus,* adults are present from May through October. Adults may consume an average of 1.7 *D. pseudotsugae* adults (Cowan and Nagel 1965) or 0.8 *D. ponderosae* adults (Schmid 1970b) per day. On *D. ponderosae* infested trees, adults are constantly moving over the bark. Females apparently lay their eggs in the bark. The larvae make their way into the galleries and prey on the larvae and pupae of the spruce beetle. The clerid larvae consumed an average of 25 *D. ponderosae* immatures during development (Schmid 1970b), so, it is probable that they consume a like number of spruce beetles. The total effect of adult and larval predation on the spruce beetle remains to be determined.

Additional dipterous predators *Erinna abdominalis* Loew, *Zabrachia polita* Coq., *Lonchaea coloradensis* Mall., are found in Massey and Wygant's (1954) extensive list of insects associated with the spruce beetle, but their importance is unknown.

Corticeus parallelus Melsheimer (Celeoptera: Tenebrionidae) is generally regarded as a phytophagous species in both the larval and adult stages. Jensen (1967) observed it eating spruce beetle eggs when they were encountered in its normal feeding on partially decomposed debris in the egg gallery.

Rhizophagus dimidiatus (Mann.) (Coleoptera: Rhizophagidae) is an abundant coleopterous associate of the spruce beetle. Most closely related species are fungus feeders. Massey and Wygant (1954) suggested this species might be predacious. It probably feeds similarly to *C. parallelus* and so can not be called a true predator. Most rhizophagids might be classified thusly.

Mites

Mites from the families Acaridae, Ascaidae, Eremaeidae and Phytoseiidae were associated with the spruce beetle on the Uncompahgre National Forest, Colorado (Sluss 1955). Sluss suggested that some of these species were predacious on the beetle but did not verify this. He believed other species were just associated with the bark or frass and were not detrimental to beetle survival.

Boss and Thatcher (1970) found only *Erynetoides sculutis* Hunter, a nonpredacious mite, associated with spruce beetles from three sites in Colorado. No predacious mites were found feeding on any stage. Boss and Thatcher thought that the mites used adults only for dissemination and did not feed on the immature stages because the tightly packed frass in the galleries

prevented access. Frass mixed with oleoresin could easily prevent mites from reaching the immature stages, but dry frass alone would probably have enough spaces to permit mite passage unless it was exceptionally densely packed.

Nematodes

Four species of nematodes, *Sphaerulariopsis dendroctoni* Massey, *Contortylenchus reversus* (Thorne), *Ektaphelenchus obtusus* Massey, and *Parasitorhabditis obtusa* (Fuchs), are endoparasites of various stages of the spruce beetle (Massey 1956).

S. dendroctoni infests both sexes of the beetle equally (Massey 1956) and may reduce oviposition of infested females by 70% (Massey 1960*). Individual trees may have as high as 75% of the beetles infested with this nematode, although a group of trees may have only 35% of the beetles infested. Male beetles help disseminate this nematode (Massey 1956).

C. reversus parasitizes the larval, pupal, and adult stages of the spruce beetle. Egg production of infested female beetles may be reduced 45% (Massey 1960*). Individual trees may have 36% of the beetles infested with *C. reversus,* but the percent of nematode-infested beetles is generally lower (maximum 23%) for a group of trees.

The effect of *E. obtusus* and *P. obtusa* on the beetle is unknown. Both have been collected from several locations in the beetles' range.

Mikoletzkya pinicola (Thorne) is an ectoparasite and is found beneath the elytra of the spruce beetle (Massey 1956). Its biology and effect are also unknown.

Several other nematode species are associated with the egg and larval galleries of the spruce beetle (Massey 1960*) but apparently do not parasitize the beetle.

Nematodes may cause the rapid decline of localized beetle infestations (Massey 1968*)—they contributed significantly to the decline of a small outbreak (McCambridge and Knight 1972). Since they seem to be one of the first indicators of the decline of an infestation, they may be worthy of study as a predictor of population trend.

Associated Scolytids

Many species of scolytids inhabit the spruce trees infested by the spruce beetle. Most of these enter the trees only after they have been attacked by the beetle (Massey and Wygant 1954), but these host trees are live and standing. A few scolytids enter downed material (usually dead) before the spruce beetle.

The most common associates are in the genus *Ips*.[3] In New Mexico and southern Colorado, *I. pilifrons sulcifrons* Wood is the common *Ips* associate; in northern Colorado, *I. pilifrons pilifrons* Swaine; in western Colorado, Utah, western Wyoming, and northern Arizona, *I. pilifrons utahensis* Wood, *I. hunteri* Swaine is an associate in blue spruce, but is also common in Engelmann spruce in Colorado and Utah. *I. perturbatus* (Eichoff) is the important species in Canada and Alaska. Along the Pacific coast, *I. tridens tridens* (Mannerheim) cohabits with the spruce beetle, while further inland from Alaska to northwestern Wyoming, *I. tridens engelmanni* Swaine is an associate. Also, in Alaska and Canada, *I. borealis borealis* Swaine is found with the spruce beetle.

Ips beetles frequently infest the upper portion of downed material, sometimes before the spruce beetle, sometimes after. Their galleries are often quite numerous, and the larvae develop rapidly so that these species seem to completely mine the phloem (fig. 8).

[3]*Dr. Stephen Wood kindly provided the following information on the distribution of the species of* Ips *and, later in this section, information on the other scolytids.*

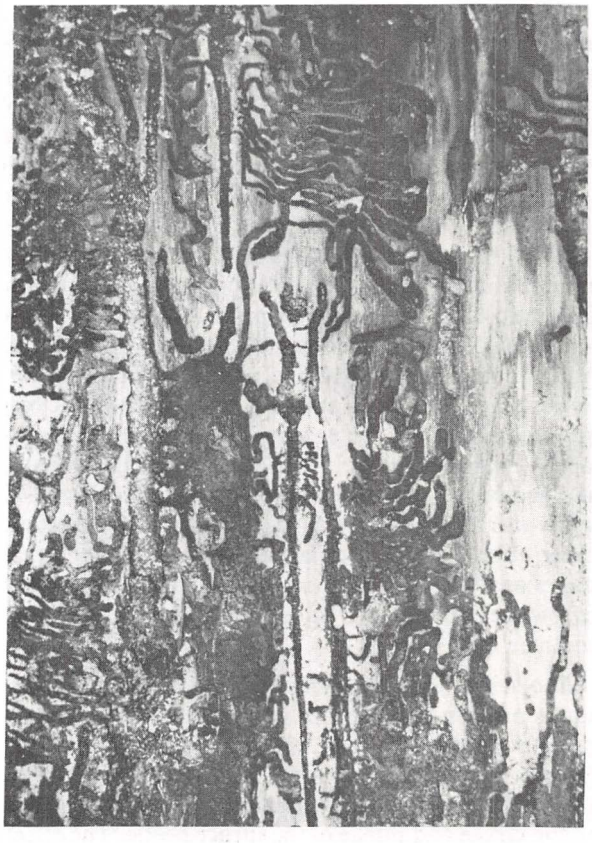

Figure 8.—*Ips* beetles commonly infest the upper surfaces of downed material, especially those surfaces directly exposed to the sun.

The upper surface of tops and cull logs in logging areas are frequently riddled. Competition between these species of *Ips* and the spruce beetle has been suggested as a limiting factor to spruce beetle populations. Competition may be important in shaded host material and in the lateral surfaces of exposed host material; otherwise, it does not seem to be a factor. Since the spruce beetle prefers shaded material and avoids fully illuminated logs, while the *Ips* species prefer the exposed material, these preferences preclude most competition. The importance of competition is yet to be determined.

Lesser known scolytids but equally abundant in some cases are species of *Polygraphus, Scierus, Dryocoetes* and *Pityophthorus*. *Polygraphus rufipennis* (Kirby) is almost as important as *Ips* and is capable of killing small, stressed trees up to about 10 inches (25.4 cm) d.b.h. *Scierus annectans* LeConte, *Dryocoetes affaber* (Mannerheim) and *D. autographus* (Ratzeburg) are found in butts and stumps. Three species of *Pityophthorus* (*nitidulus* (Mannerheim), *occidentalis* Blackman, *bassetti* Blackman) are found in the branches of spruce beetle-infested trees.

Effects of Infestation

A spruce beetle infestation has immediate and long-term effects on the spruce-fir stand. The immediate effect changes the stand structure and composition. The long-term effect comes from successional changes in the stand caused by the death of the spruce as well as the associated effects on water yield, forage production, wildlife populations, and fire hazard.

Stand Structure and Composition

Stand structure is modified by spruce beetles. They reduce the average age of the surviving trees, lower the average diameter and height of the stand and the spruce component, lower the density, and leave suppressed and intermediate trees as the dominant or co-dominant spruce (fig. 9).

The number of live trees may be drastically reduced—from less than 1 per acre to 99% of the trees over 10 inches (25.4 cm) d.b.h. During the White River outbreak, 99% of the overstory trees were killed throughout thousands of acres. Despite this, scattered, single, medium diameter trees survived within the devastated stand. In Alaska, mortality of white spruce more than 5.0 inches (12.7 cm) in diameter exceeded 90% on some sites but generally averaged 65% over 70,000 acres (Baker and Kemperman 1974). In Arizona, about 5% of the trees over 5.0 inches (12.7 cm) d.b.h. were killed (Frye and Flake 1971). However, a greater percentage of the larger trees died than did the more numerous intermediate-sized trees. Tree losses were highest in areas with the largest trees and highest basal area (Frye and Flake 1971).

Figure 9.—This dead stand on the White River Nat. For., Colo., exemplifies typical mortality to the dominant trees during an outbreak.

The number of seedlings and saplings is not immediately affected unless the infestation is logged. Without logging, an insignificant few will be killed or injured in subsequent years by the falling of the dead overstory. Generally, the existing seedlings survive better after the overstory trees are killed. Existing seedlings will compete with herbaceous vegetation; this competition will become more intense in 2 or more years after the death of the overstory trees, when the herbaceous vegetation has had time to also respond to the change in conditions.

Seedlings may become established in the first three years after the trees are killed but then be unable to survive competition from the dense herbaceous vegetation which also develops.

With logging, established seedlings can be reduced in number to well below the minimum level for adequate stocking (300 per acre or 0.4 ha) but this varies with the intensity of the logging. If logging has re-

duced the number of seedlings below the adequate level, then planting may be desirable. Spruce seedlings may need partial shade (Ronco 1961). Full light intensity impairs their physiological functioning and causes high mortality (Ronco 1961). Drought and frost heaving are not important mortality factors to planted spruce seedlings (Ronco 1961).

Species composition can be altered. In Colorado, stands which were 90% spruce-10% fir in the overstory before the outbreak became 20% spruce-80% fir after the White River outbreak (Schmid and Hinds 1974). In Alaska the white spruce-paper birch (*Betula papyrifera* Marsh) ratio changed from 77%-22% to 55%-45% respectively (Baker and Kemperman 1974). Most infestations cause compositional changes over a less extensive area than the two previous examples, but they can be just as intensive in a small area, so, the species composition within a portion of a stand may drastically change even though the overall composition of the stand is only slightly altered.

There are immediate and long term effects of infestations on species composition of seedlings. Existing spruce seedlings benefit more from the opening of the stand than do fir seedlings. Immediate composition will remain unchanged. Subsequent composition depends on the intensity and extent of the outbreak.

Succession

The characteristics of potential outbreak stands and the changes in species composition caused by beetle infestations provide a basis for speculating on ecological succession in the spruce-fir type (Schmid and Hinds 1974). Daubenmire (1943) classified spruce-fir as the climatic climax. Alexander (1974*) predicts that spruce is the climax species in the central Rockies, and will eventually replace the fir if the stand is not disturbed. Miller (1970) correlated age structure in spruce-fir stands in the central Rocky Mountains with spruce beetle outbreaks, but did not speculate on stand succession. Schmid and Hinds (1974) agreed with Miller, but further suggested that the combined forces of spruce beetles, and *Dryocoetes confusus* Swaine and associated fungi alter the status of the spruce and fir components over the years, first toward fir, then toward spruce, and then back to fir as each species matures and spruce beetles periodically reach outbreak status.

The development of a spruce-fir forest over several centuries might be as follows: Assume a stand like one of those on the White River National Forest after the beetle outbreak in the 1940's; 80% fir-20% spruce in trees larger than 3 inches (7.6 cm) d.b.h., and the same or a higher percentage of fir in the seedling class. Both species grow rapidly. Fir continues to predominate and slightly increases its component in the overstory. As the overstory firs reach a diameter of 16 to18 inches (40.6-45.7 cm) d.b.h., or 125 to 175 years, they begin to die and fall out of the overstory. Why fir dies is not completely understood, but Swaine (1933) cites *D. confusus* Swaine as a mortality agent in British Columbia, and Molnar (1965) identified a *D. confusus*-fungus complex as killing 6- to 15-inch (15-38 cm) fir. The total BA curve reflects these decreases due to the loss of fir (fig. 10). Younger spruce and fir use these unoccupied sites and increase in size, but the spruce component in the overstory increases proportionately more than the fir.

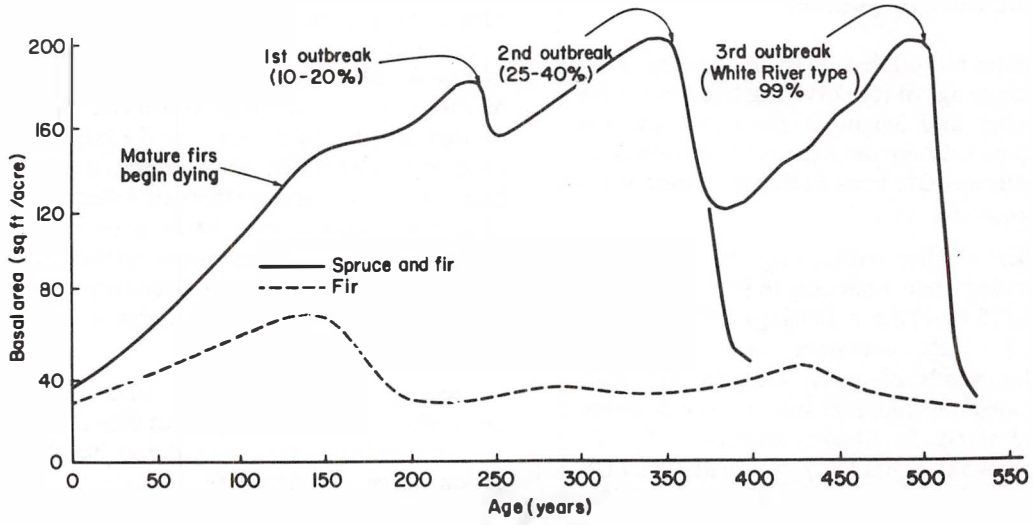

Figure 10.—Hypothetical curve of succession in the spruce-fir forest using basal area as an indicator of stand structure.

Meanwhile, more seedlings are becoming established, so, the spruce component is increasing slightly because of two factors. First, even though fir seedlings vastly outnumber spruce seedlings, the original removal of the canopy by the beetles favors the less tolerant spruce more than it does the highly tolerant fir. This allows spruce seedlings to compete more vigorously with fir, whereas, prior to the outbreak, fir was in the more advantageous position. Second, animals or other factors heavily damage more fir seedling leaders than spruce leaders, so spruce gains valuable height on fir. Eventually, since spruce lives longer and grows larger (LeBarron and Jemison 1953), it becomes dominant. At that point, the fir occupies a smaller percentage of the canopy.

Total BA begins to increase rapidly and proceeds toward the potential of the site as the maturing spruce grow. At periodic intervals spruce beetle outbreaks reduce the total BA and the spruce component, as Miller (1970) suggests, but the initial outbreaks kill less than 50% of the spruce—probably 10% to 20% (Frye and Flake 1971), or 25% to 40% (Sudworth 1900b) —before the beetle population subsides because of natural factors.

Such outbreaks are probably examples of the "pocket biology" of the spruce beetle—a situation where the beetles reach outbreak status in a generally immature stand with pockets of larger diameter trees. The spruce component decreases and fir increases, but the spruce still occupies more than 50% of the live BA. As the stand recovers after each outbreak, the stand tends more toward a single story. The stand continues to grow and approaches maximum BA. It is then highly susceptible to spruce beetle outbreaks. Eventually, given the moisture and wind conditions characteristic in the central Rockies, blowdown occurs. Spruce beetles develop to outbreak proportions in the downed material, and attack the surrounding standing spruce, killing it so that the stand becomes fir, and the transition from predominantly fir to spruce to fir is complete.

The trend of the total BA curve after the stand reaches the site potential and sustains an outbreak is open to further investigation. It may proceed in a wavelike trend resulting from intensive outbreaks, continue downward from an expanding initial infestation, or remain relatively static with minor fluctuations due to endemic infestations. Historical data and knowledge of spruce-fir stands suggest the wavelike trend is probably the most likely.

Watershed Relationships

The effects of outbreaks relate to streamflow, interception, and transpiration. Love (1955) estimated that streamflow increased more than 2 inches (about 22%) annually for the entire watershed, or a 7.7-inch depth (about 75%) for the 226 square miles (58,534 ha) of beetle-killed spruce in the latter years of the White River outbreak. He attributed this increase to reduced interception and transpiration. The dead trees permitted a greater accumulation of snow on the forest floor which, in turn, yielded more streamflow because the dead trees did not evapotranspire (Love 1955).

Bue et al. (1955) discount the effect of the White River outbreak, and indicate that some factor(s) not associated with the death of the trees was responsible for the change in streamflow. Mitchell and Love (1973) reanalyzed the White River data and concluded that there was a significant increase in annual flow, 1.6 to 1.9 inches (about 16% for the entire watershed, or 5.5 to 6.4 inches (about 58% from the beetle-damaged area)) although the increase was less than Love's 1955 analysis estimated. Bethlahmy (1975) also concluded that the most logical explanation for the increase in water yield relates to changes in vegetation cover, i.e., the vast mortality of the overstory spruce.

The effect of an outbreak is probably similar to the general changes that occur after logging, with minor differences caused by the standing dead trees. Leaf and Alexander (1975) noted that total snow storage was not changed but was distributed differently following harvesting. More snow (+30%) accumulated in the logged areas while less snow (-20%) accumulated in the uncut forest. The length of the snowmelt season remained the same, but snowmelt increased in the early part of the season and decreased in the latter part. Peak streamflows will not increase appreciably when 40% of the watershed is patch cut. Evaporation is greater from the snowpacks in the logged areas than from the uncut forest. Evapotranspiration and interception losses were reduced in proportion to amount of forest cover removed. Water yields were highest where the openings were kept to less than eight tree heights in diameter. On a watershed basis, the redistribution of snow into clearings increases runoff because less water is needed to satisfy soil moisture deficits due to reduced transpiration loss after tree removal. The increase in water yield will last for 30 years or longer depending on how soon the forest cover density reaches its maximum value.

How similar an infested area is to a harvested watershed depends on the extent and intensity of the infestation. Assuming the area affected by an outbreak approaches the size of the cut area discussed in Leaf and Alexander (1975), then the following appear logical: (1) snow deposition among dead trees should be slightly less than in a clearcut opening because the dead trees will intercept some snow and prevent it from accumulating on the ground; interception will decrease

as the branches weather and drop to the ground; (2) evapotranspiration should be the same as that of the cut areas, while interception loss should be slightly greater; (3) standing dead trees should inhibit winds from scouring out the snow, so, the size of an infested area should not be a factor; (4) the snowmelt season should begin somewhat later than that of clearcut areas because the dead trees will provide some shade; (5) the pattern of streamflow should correspond closely to the pattern of the cut area; (6) water yields should be slightly less than in cut areas because of the slightly greater interception loss; (7) the increase in water yield should last as long as it would in selectively cut stands; (8) soil erosion should be negligible.

Forage Production

Relatively little forage is found in mature spruce-fir forests (Yeager and Riordan 1953). In green stands, mature spruce and fir dominate all other vegetation, using a large portion of the available light, moisture, and soil nutrients (Yeager and Riordan 1953). Stands on dry slopes are more or less brushless, while those on moist sites have varying densities of undergrowth. Under a spruce-fir canopy, the predominate ground cover in green forests is whortleberry *(Vaccinium).* On dry sites, a shrubby buffaloberry *(Shepherdia),* and scattered composites, *Arnica* and *Aster,* are present. On moist sites, mountain bluebells *(Mertensia),* larkspur *(Delphinium),* and butterweed *(Senecio),* are common, while wild currants *(Ribes)* and elder *(Sambucus)* are common shrubs.

Comparing green stands to beetle-killed stands, grasses and sedges showed increased density in dead stands (Yeager and Riordan 1953). Forbs were 2.3 times more numerous in dead stands, while browse (woody) plants showed a steady, unexplainable decrease. The greatest density, number of species, and index of occurrence of plants was in beetle-killed stands (Yeager and Riordan 1953).

How long forage population will continue to increase after an outbreak has not been determined. Under outbreak conditions like the White River, it should increase each year for several years and reach maximum production in 3-5 years (Currie 1977*). Annual production would then fluctuate around this maximum level until the spruce and fir seedlings begin to compete. If the site is occupied with advanced regeneration, it should begin competing in 50 years. If the site is relatively unoccupied with advance regeneration, forage production may be unaffected for considerably more than 50 years, which may preclude the establishment of seedlings.

Forage production in beetle killed stands is probably similar to that of logged areas. Wallmo et al. (1972) found 853 ovendry pounds per acre (388 kg per 0.4 ha) on cut strips versus 391 pounds per acre (178 kg per 0.4 ha) on uncut strips, 16-18 years after cutting. In terms of deer forage, 509 pounds per acre (231 kg per 0.4 ha) were present on cut strips, and 346 pounds per acre (157 kg per ha) on uncut strips (Wallmo et al. 1972). They also estimated that forage supplies were 47% greater on the cut strips.

Wildlife

The effects on each species depends on that species' requirements and the intensity and extensiveness of the infestation. Where only a few trees are infested on 1-2 acres (< 1 ha), the changes would be insignificant. Where the outbreak reaches the intensity and extensiveness of the White River outbreak, then significant changes would be expected. Most of the following information relates to major outbreaks. Since trends in mammal and bird populations have not been adequately studied, such expected changes are opinions based on knowledge of the animals' requirements.

Elk *(Cervus elaphus* Linnaeus), and deer *(Odocoileus hemionus* (Rafinesque)), benefit from beetle outbreaks because forage production increases. Wallmo (1969) notes that deer use was significantly higher in logged strips than in adjacent uncut forests 10 years after cutting. This is a response to increased forage on the cut area—a condition also to be expected beneath an infested stand. Although summer range is not critical for elk and deer in Colorado, the increased abundance and diversity of their forage in a large beetle-killed area could result in greater accumulations of body fat, and thus better enabling them to survive on their critical winter range which is below the spruce-fir habitat.

Red squirrels (*Tamiasciurus hudsonicus* (Erxleben)), were adversely affected because of the loss of spruce seed (Yeager and Riordan 1953). Chipmunks *(Eutamias* spp.), and meadow mice (*Microtus* spp.), increased appreciably, presumably because of the increase in grasses and forbs (Yeager and Riordan 1953). Although white-footed mice (probably deer mouse *Peromyscus maniculatus* (Wagner)), and boreal redbacked mice (voles) *Clethrionomys gapperi* (Vigors), decreased and increased respectively, these changes were independent of the beetle outbreak and probably reflected cyclic changes (Yeager and Riordan 1953). Other small mammals were either unaffected or the data was insufficient to detect an effect.

Since meadow voles (*Microtus pennsylvanicus* (Ord)), and redbacked voles are the most important food of the pine marten *(Martes americana* (Turton)), and they increased, then pine marten should increase.

However, marten prefer densely stocked stands of subalpine fir (Koehler et al. 1975), so, loss of canopy cover is detrimental. Also, marten activity is greatest in stands with less than 30% canopy cover when snow depth is less than 12 inches (30 cm) (Koehler et al. 1975). Snow accumulates to several times this depth in green spruce-fir and even greater depth in beetle-killed stands (see Watershed section). This would limit marten usage. Thus, the increase in food may have been counterbalanced by the loss of cover leaving marten populations about the same.

Snowshoe hares (*Lepus americanus* Erxleben) showed no response to the White River outbreak (Yeager and Riordan 1953). Coyotes, (*Canis latrans* Say), a predator of rabbits, were not observed.

Woodpecker populations initially would benefit from a large outbreak and increase due to the increase in spruce beetles. After an outbreak subsides, woodpeckers would still benefit from the large numbers of secondary insects (cerambycids, ants, other scolytids) present, but this would only last 2-3 years. After these insects decline, woodpecker populations would decline because of the lack of food. Even though more nesting sites would be available in the snags, the lack of food counterbalances this benefit.

Other insectivorous species such as nuthatches (*Sitta* spp.), and brown creepers (*Certhia familiaris* Linnaeus) would be similarly affected. Initially they benefit even though the spruce beetle is not their primary food, but, as the needles and bark fall off, available food and cover would be greatly reduced so their numbers would decline.

Pine grosbeaks (*Pinicola enucleator* (Linnaeus)) were adversely affected because of the loss of spruce seed (Yeager and Riordan 1953). Spruce grouse (*Canachites canadensis* (Linnaeus)) would also decline because of the loss of cover and winter food (spruce buds).

Owls and hawks would not be affected in the first years (1-2) after an outbreak but would increase in later years due to the increase in mice populations and to a lesser extent, nesting sites.

The Gray jay (*Perisoreus canadensis* (Linnaeus)) appeared unaffected (Yeager and Riordan 1953).

Fire Hazard

The importance of the fire hazard in a beetle-killed spruce-fir stand has been exaggerated and is less than for other beetle-killed timber types, especially the pine. Miller (1970) noted that evidence of widespread fires between 1750 and 1930 is lacking on the White River Plateau. One large fire in 1879 was started by Indians. Mielke (1950) stated that no large fires have burned in the spruce-fir in Colorado since 1900. Since the White River Outbreak, the only fire of significance (started by elk hunters) burned 4,500 acres (1,821 ha) in 1975 in the beetle-kill area. Based on this evidence, Watt's testimony that, if the spruce beetle was not controlled, a very serious fire hazard would be created on the White River Plateau (U.S. Senate 1952) exaggerates the danger.

Unquestionably, spruce beetle outbreaks create a large fuel source, and the snags are potential lightning rods. Cahill (1977) estimated that more than 40% of his study area in the White River outbreak area had 55 or more tons of dead fuel per acre (49,895 kg per 0.4 ha), and 97% of the forested area had 55 snags per acre (0.4 ha)—this some 30 years after the outbreak. However, most storms are accompanied by rainfall which dampens the vegetation and prevents development of a widespread fire. Also, frequent showers during the fire season create a moister environment—one reason why spruce grows there. Thus, the hazards seem to be negated by the moister conditions.

Deterioration

Beetle-killed spruce fall at a slow rate. Mielke (1950) found 84% still standing after about 25 years—rate of fall was 0.7% per year. Schmid and Hinds (1974) found an average rate of 1.5% per year for the White River outbreak and 1.3% per year on the Aquarius Plateau (Mielke's study area). The rate of fall seems to increase slightly with time.

Trees fall mainly because of root and basal rots. Both are equally important. Windthrow was not important in the infestation on the Aquarius Plateau (Mielke 1950), but it accounted for 25% of the trees in the White River outbreak area after 20 years (Hinds et al. 1965).

Although Mielke (1950) rarely found decay 1-2 feet (.3-.6 m) above ground, it can still be present. Three years after being infested, the moisture content of the heartwood and sapwood of standing trees was generally below 22%, so, trunk decay fungi were unable to develop (Mielke 1950). However, trunk decay fungi can develop where there is sufficient moisture, and the checks in the bole may collect enough moisture for local pockets of the fungi to develop (Hinds 1977*). In the Colorado study by Hinds et al. (1965), *Fomitopsis pinicola* (Swartz ex Fr.) Karst, extended upward for 10-15 feet (3-4.6 m). Furthermore, the basal section of the bole is frequently wetted by rain or snow, enabling basal decay fungi to readily develop. These fungi contribute to the weakening of the bole, decreasing resistance to windthrow.

Decay averaged about 1% per year; after 10 years, 11% of the volume was lost (Hawksworth and Hinds 1959). *Phellinus pini* (Thore ex Fr.) Pilat, a heart rot, was the most important fungus, accounting for 42% of all decay (Hawksworth and Hinds 1959). *P. nigrolimitatus* (Rom.) Bourd. et Galz caused 50% of the butt rot, while *F. pinicola* accounted for 66% of the sap rot (Hawksworth and Hinds 1959).

Later in the study, decay in standing trees averaged 12% of the volume within 20 years (Hinds et al. 1965). *P. pini* accounted for 3% of the total cubic foot volume and 24% of the total decay volume (Hinds et al. 1965). Also, *P. nigrolimitatus* had caused 6% of the total decay volume and 26% of the butt rot, while *F. pinicola* caused 9% of the total decay volume and 31% of the sap rot (Hinds et al. 1965). The differences in the rate of decay and the percent decay accounted for by each fungus in the two studies is related to the rate of development of the fungi and sampling procedures. Fungi develop rapidly after the trees die, and then their development levels off. As time passes, the trees with greater amounts of decay fall (fig. 11), while the sounder trees remain standing. These trees are thus removed from future sampling, so, later results tend to show lesser amounts of decay.

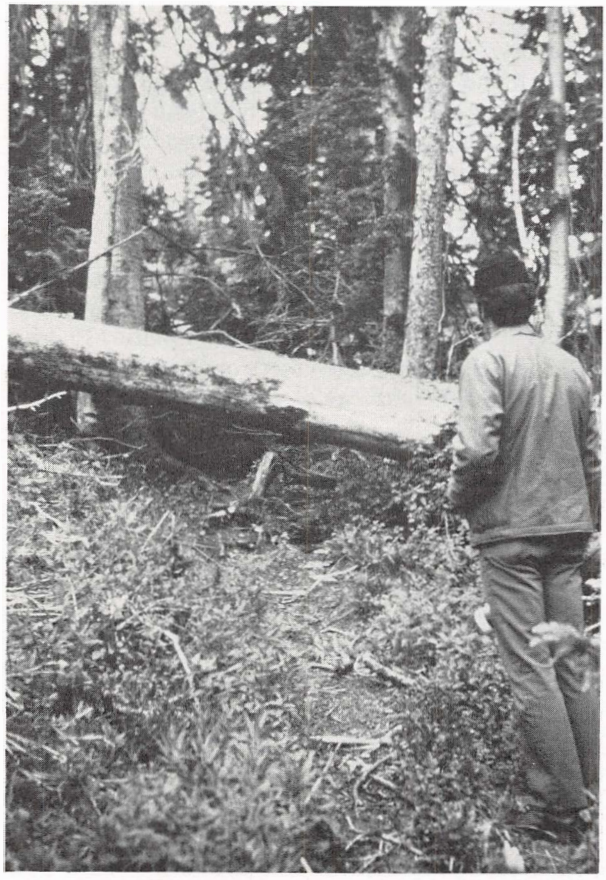

Figure 11.—Beetle-killed trees may stand for more than 25 years but eventually they fall, sometimes blocking trails or becoming a hazard for hikers.

Fallen trees in contact with the ground decay in 5 years (Schmid and Hinds 1974).

Checking commonly develops in beetle-killed spruce. Twenty-five years after infestation, 65% of the trees had one large season (deep) check and 15%-20% had two (Mielke 1950). Fifteen percent of the trees developed no large season checks but did have numerous small, shallow checks. Losses from the shallow checks are minimal since they can be slabbed off. Losses from the season checks were not high and may be compensated for by the reduced cost of logging (Mielke 1950). The season checks are a factor only when the trees are cut for lumber.

The development of checking varies among trees. Some begin checking before needle fall, i.e., 1-2 years (Mielke 1950). A tree infested in July and debarked by woodpeckers during the winter may be unmerchantable 1 year later (Hester 1960*). Nelson (1954) indicates that logging ceased about 3-5 years after the trees were infested, so apparently checking was complete in 5 years. Checking ceases after the wood dries. As noted by Hester (1960*), woodpecker activity may influence checking because the removal of the bark would accelerate the drying process. Perhaps those trees that incur heavy woodpecker feeding develop checks the first year while those without woodpeckering develop checks in 2 or 3 years.

Wood Products

Salvage of beetle-killed spruce can proceed for many years after the trees are killed depending on the product to be derived. Timber for sawlogs remained merchantable for about 5 years, then enough trees developed radial checking to make them unmerchantable for small sawn boards (Nelson 1954). Trees that have been dead for more than 5 years are currently being cut for use as house logs in log homes in southwestern Colorado. High quality particle board can be produced from beetle-killed Engelmann spruce even though it has been dead 10-12 years (Mueller 1959). Both the flakeboard and hammermilled type had strength properties competitive with particleboards from other species (Mueller 1959). The same timber may remain suitable for pulp for 20 or more years (Nelson 1954). Cubic foot volume per Engelmann spruce from the Routt National Forest, Colorado, ranged from 15 for a 10-inch (25 cm) tree to 196 for a 29-inch (74 cm) tree (Mogren 1958). The average cord consisted of 2.6 beetle-killed trees when such trees were utilized to a 5-inch (13 cm) top (Mogren 1958). Some 50 years after infestation, spruce were being cut for mine props (Schmid and Hinds 1974).

Each beetle-killed spruce deteriorates differently, so, merchantability of a stand is variable (see Deterioration). Enough trees may become unusable within a few years, causing the salvage cutting in the stand to become uneconomical. However, by designating a felling and skidding pattern like the herringbone design, as suggested by Schaeffer (1954), harvesting can proceed faster, more beetle-killed area can be covered, and harvesting losses in the residual stand can be reduced.

Detection and Evaluation

The forest manager needs to know if spruce beetles are present in his management area, their distribution, and the potential significance of the infestation. Translated into the terminology of the pest manager, these general questions mean detection and biological evaluations. Detection is the discovery of infestations in their earliest stage of buildup. A biological evaluation is an appraisal of the current and potential significance of the infestation.

Detection and evaluation of spruce beetle infestations are usually accomplished by surveys. The objectives of surveys are (1) to find incipient and outbreak type spruce beetle infestations, (2) to find areas of forest damage (blowdown, broken-off trees) that may contribute to an outbreak, (3) to measure beetle populations and their trend, (4) to estimate the number of infested trees within each infestation, and (5) to determine their concentration (Wilford 1965*).

In the past, the distinction between detection and evaluation has not always been clear because detection information was gathered during an evaluation survey, or because the two types of surveys were made together. This is not inherently bad, but it does create some confusion as to the allocation of costs and the type of information to be gathered on each type of survey. For this report, the discussion of detection (detection surveys) will be confined to the discovery or location of infestation. The gathering of all other information will be considered as part of the evaluation process.

Detection

Infestations are detected through a combination of ground and aerial observations. Detection on the ground can be accomplished by field surveillance, scouting, or a systematically designed survey. Field surveillance is the technique of being alert in the forest—constantly observing the trees for signs of an abnormal condition. Forest workers do this as part of their regular work. Scouting is also a means of detecting infested trees. Scouting follows a random course with no preset pattern and is the most feasible, relatively inexpensive method of detection (Wilford 1965*). Systematic ground surveys have also been used for detection although this type of survey has been used sparingly since the White River outbreak. They differ from scouting in that they follow predetermined cruise lines. Since definite routes are taken, the systematic design provides better knowledge of the distribution and location of the infested trees. Both scouting and the systematic plan record essentially the same information. The details of the survey, including equipment, organization of the survey party, classification of infested trees, etc., are thoroughly outlined by Wilford (1965*).

Aerial surveys are also used to detect spruce beetle infestations, especially in remote roadless areas. Such areas can be more rapidly surveyed from the air than from the ground (Wilford 1965*). Suspect areas are usually inspected from light planes flying parallel flight lines during the summer (fig. 12). Once a suspected area is located, a ground check is made. If an infestation is uncovered, then more intensive ground surveys are made.

Aerial surveys use both fixed-wing and rotating-wing aircraft. Fixed-wing aircraft can be used to detect large infestations in inaccessible areas, but are less adequate than helicopters for detecting small, incipient infestations (Landgraf 1960*). Helicopters also offer the following advantages over fixed-wing planes: (1) they can land and take off from parks or exposed

Figure 12.—W. F. Bailey sketch mapping spruce beetle infestations from a light plane. "Beetle" has surveyed Colorado's spruce-fir type for more than 20 years.

ridges which enables an observer to check a suspicious area that might be quite distant from the road; (2) they are more versatile aircraft and can operate at speeds as low as 20 miles per hour (30 km per hour) at tree-top level, in narrow drainages, although normal operating speeds are 40-50 miles per hour (64-80 km per hour), (3) they have superior forward and lateral visibility, and (4) they fly in more turbulent air conditions (Landgraf 1960*). Helicopters may also be more economical if ferry time is minimized and maintenance is performed in the field. However, on an hourly basis, helicopters are much more expensive.

The benefit-cost relationship of aerial detection surveys has always been questionable. Wilford (1965*) claimed that such surveys were too costly unless the aircraft was used concurrently for other insect surveys or forest functions. Since infested trees may have differential rates of fading, no fading for more than one year, or needle fall without a color change (Wear et al. 1966), detection can be difficult and the worthiness of the survey questionable.

Obviously, a favorable benefit-cost ratio depends on the successful detection of infested trees which is influenced by the status of the infestation. Low level infestations (not outbreaks) are most often detected from the ground (Wilford 1965*). Such infestations may be more conspicuous to aerial observers in winter when bark chipped off by woodpeckers builds up around the tree bases. Then, detection from a helicopter may be possible; less likely from a fixed-wing plane. However, even helicopter flights to discover such infestations are not usually feasible because the probabilities of missing infestations are too great (Wilford 1965*). Outbreaks are readily detected from the ground and more easily recognized from the air than low level infestations. Under outbreak conditions, detection becomes more certain and the benefits of the aerial survey more positive. The more favorable points under these conditions are counterbalanced by the idea that if the infestation reaches the outbreak level before it is located, our detection method isn't very satisfactory. Considering this evidence, current systematic aerial surveys of entire national forests may be unjustified even though they have been used more frequently in recent years than ground surveys.

In the future, scouting surveys around cutting areas, windthrow, road construction and other human activities may be the most frequently used detection technique. Lacking disturbed stands, surveys should be concentrated in high hazard stands. Aerial surveys with light planes will be used on a more limited basis because of the cost. Systematic ground surveys for detection alone will rarely be used because of their cost and because this type of survey gathers the type of information more common to the evaluation process. New areas of infestation may be located under a systematic evaluation survey, but this detection information will be incidental to the main purpose of the survey. These latter instances exemplify the overlap between detection and evaluations.

Evaluations

Spruce beetle evaluations are composed of three different aspects: (1) appraising the significance of the infestation (biological evaluation), (2) determining the cost-benefit relationship between values threatened and cost of suppression (benefit-cost evaluations), and (3) determining possible environmental impacts of the infestation and of suppression measures (environmental impact evaluations). This report is concerned mainly with the appraisal of the significance of an infestation and the techniques used therein.

Since biological evaluations seek to appraise the current and potential significance of an infestation, significant quantities of data must be gathered to make an appraisal meaningful. This is usually accomplished by (1) examining the brood in infested trees (fig. 13),

Figure 13.—Trends in beetle populations are based on examinations of brood in the bark. D. D. Lucht clearing branches prior to extraction of the bark sample.

and (2) surveying the infested stands. Frequently in the past, however, the evaluation consisted only of examining the spruce beetle brood and then using the numbers counted in a predictive sampling plan. Surveys to determine the size and intensity of an infestation were performed later, if additional stand information was desired or if the trend prediction indicated an increasing population.

A procedure for predicting trends in spruce beetle populations in standing trees is available, but none are available for populations in logging residuals and windthrow. Knight's sequential sampling plan permits populations in standing trees to be evaluated in June and in August-September (Knight 1960b). The June sampling can determine if control actions are needed immediately. Decreasing populations require no treatments; static and increasing populations are considered treatable. The August-September sampling determines whether the emerging beetles will kill the next year—(1) more trees than are presently infested (increasing), (2) about the same number (static), or (3) fewer trees (decreasing). The sequential plan is currently used in conjunction with a basic stand description to forecast population trends.

Predictive sampling plans are not available for logging residuals because of the high variability in brood. Brood counts vary between surfaces within cull logs, between logs, tops and stumps, and between transect lines (Schmid 1977). This complicates the development of a common denominator which would give a trend for all categories of logging residual (logs, stumps, tops) from the sampling of only one. Individual schemes could be developed for each category, but this may not be practical.

Predictive sampling plans are also not available for blowdown. A plan being developed should have a greater chance of being useful, since only one category of infested spruce is involved.

In addition to the trend in the beetle population, information on the size and intensity of the infestation, as well as the stand structure, is important. This information can be gathered from systematic ground surveys; the objectives of the survey dictate its sampling design.

Circular plots can be used to estimate the intensity of an infestation. One-tenth-acre (0.04-ha) plots established at 2-chain (40-m) intervals along parallel cruise lines generally give the most accurate results (Knight et al. 1956). The 1/20-acre (0.02-ha) plot is more advantageous when areas are heavily infested. Plots larger than 1/10-acre and strip methods are less accurate than the 1/10-acre plot (Knight et al. 1956). In recent years, the variable plot method has been used with a 20-basal-area factor prism on standard parallel cruise lines (Frye and Flake 1971, Acciavatti 1974). A combination strip and variable plot cruise may yield the most information for the money spent.

In the 1960's, aerial photos could not be recommended for surveys to determine Engelmann spruce mortality (Wear et al. 1966). Recently, large scale (1:2250) 70-mm infrared aerial photography has proven feasible for estimating the number of dead, formerly infested spruce (Lessard and Wilson 1977). Interpretation of such photography is most accurate when evaluated by experienced interpreters. However, the number of beetle-killed trees may be overestimated because snags (trees killed by unknown causes) are tallied as beetle-killed. Since the interpreters are counting trees bereft of foliage, this photography is good for assessing the extent and intensity of an outbreak but is not adequate for estimating the number of currently infested trees.

Moderate scale (1:8000) color aerial photography has also proven effective for estimating dead, formerly infested trees. (Rush et al. 1977). This scale of photography has the disadvantages inherent in the scale of photograpy of Lessard and Wilson (1977). Both types of photography also have the problem of underestimating dead trees when a stand is multistoried and the smaller dead trees are hidden below the dominants.

Suppression

Chemicals

Although much has been learned of chemicals and spruce beetles, the constantly changing legal status of chemicals prohibits definitive recommendations. What can be applied today may be prohibited tomorrow. Therefore, chemicals will be discussed regardless of whether they are currently registered or not. For current status, interested parties should contact their state or federal pest management office.

Dichlorobenzene.—The fumigant dichlorobenzene was toxic to the spruce beetle and was used with good effect on the control projects until it was replaced by ethylene dibromide (Nagel 1960*). Dichlorobenzene was obtained as a mixture of para and ortho isomers. For best results the ortho content had to be about 60% to hold the para in solution during the coldest treating weather (Nagel 1960*). Dichlorobenzene was replaced because its vapors were particularly disagreeable at high altitudes, and fuel oil was the dilutant (Nagel 1960*). Fuel oil added a six-fold volume to the

transportation burden, and, with water abundantly available in most of the spruce stands, this was not economical.

Eight or five pounds of orthodichlorobenzene in sufficient fuel oil to make 5 gallons (19 l) resulted in 99% beetle mortality when sprayed on logs with mature brood. The heavier dosage rate was also tested against hibernating adults in the bases of standing trees and resulted in about 100% mortality. Tests on a limited number of standing trees with 4 and 8 pounds (1.8 and 3.6 kg) of orthodichlorobenzene resulted in 92% and 94% mortality, respectively. From 1950-1952, it was used on the control projects in western Colorado (Massey and Wygant 1954).

Napthalene and Trichlorobenzene.—Chlorinated naphthalene and trichlorobenzene were not effective on beetles in logs at 1-4 pounds per 5 gallons (0.5-1.8 kg per 19 l) of carrier (Massey et al. 1953).

Ethylene Dibromide (EDB).—EDB was used extensively to fumigate spruce beetles during the White River outbreak when the development of an emulsion was completed in 1951 (Nagel 1960*). Addition of epichlorohydrin inhibited the erosion of storage containers and allowed EDB to be held in readiness for longer periods.

EDB applied in concentrations of 0.75 and 1.5 pounds per 5 gallons (0.3 and 0.7 kg per 19 l) of fuel oil to standing trees with all brood stages resulted in 98% and 100% mortality, respectively (Massey and Wygant 1954). Although mortality was 97% at 5 feet (1.5 m) above ground, it was considerably less than 50% at 15 feet (4.6 m) (Massey et al. 1953). The higher up the tree, the less effective EDB was, even with concentrations of 3 pounds per 5 gallons (1.4 kg per 19 l) of carrier. This suggests an application problem rather than a lack of effectiveness of the compound. Emulsions of EDB in water applied to logs and standing trees generally resulted in 95% or more mortality in test cases. The emulsion containing 3 pounds (1.4 kg) of EDB was used in the spruce beetle control project in Colorado. One pound of EDB per 5 gallons (19 l) of fuel oil is considered effective in British Columbia (Grant and Cottrell 1968).

More recently, concentrations of 0.25, 0.75, and 1.25 pounds of EDB per 5 gallons (0.1, 0.3 and 0.6 kg per 19 l) of fuel oil caused 100% mortality in limited numbers of cull logs when applied to the point of runoff (Schmid 1972).

Dichloroethyl Ether.—Dichloroethyl ether in oil solutions were just as effective as EDB against all stages of the beetle (Nagel 1960*). Four pounds (1.8 kg) of the compound per 5 gallons (19 l) of fuel oil caused 100% mortality in standing trees when applied in late September (Massey et al. 1953). Dichloroethyl ether did not corrode iron or solidify until about -55° F (-48° C) and was quoted at half the price of EDB in 1955 (Nagel 1960*). Its disadvantages—flash point of 131° F (55° C), more dichloroethyl ether needed than EDB per 5 gallons, and disagreeable odor—may have eliminated its use.

Fuel Oil.—Fuel oil by itself caused mortality against broods in cull logs (Schmid 1972). In later testing, mortalities ranged from 76% to 100%. The fuel oil was more effective when the brood was mostly larvae rather than callow adults.

DDT.—A 4% solution of DDT in fuel oil applied to infested logs and standing trees resulted in 100% mortality in the adult stage but 97% and 76% mortality in the larval stage in both types of host material respectively (Massey and Wygant 1954). Tests on host material predominantly infested with larvae and pupae generally resulted in less than 50% mortality. DDT did not act as a fumigant, so, it was rather ineffective on the larvae within the phloem. Adults received a lethal dose as they emerged from the bark. Mortality was not accurately determined because the adults were still capable of departing from the log even though they died later.

Benzene Hexachloride (BHC).—An emulsion of BHC (enough BHC in the oil to give 0.46% of the gamma isomer) resulted in 92% and 90% mortality of the adult and 97% and 92% mortality of the larval stages in logs and standing trees respectively (Massey and Wygant 1954). However, BHC in oil alone resulted in less than 50% mortality.

Silvisar 510.—Silvisar 510 (S 510) was developed as a herbicide for thinning stands of conifers and hardwoods. The lethal component in S 510 is cacodylic acid, a highly water-soluble pentavalent arsenic compound. Cacodylic acid kills the crowns of trees mainly by desiccating the meristematic tissues of buds and new twigs (Smith 1966). It also affects the abscission layer of the leaf. S 510 has a low order of mammalian toxicity and is relatively nonirritating to skin and eyes (Chansler and Pierce 1966).

S 510 has come to be commonly called cacodylic acid because its lethal ingredient is the acid. This has led to some ambiguity because other trade name chemicals (Ansar 160, Silvisar 550) contain cacodylic acid but have different concentration of cacodylic acid as well as different formulations per unit of solution. Even with S 510, the concentration of cacodylic acid has varied (see footnotes of Buffam and Yasinski 1971, Buffam 1971). Since different formulations may produce significantly different effects, it is important to specify which cacodylic acid containing solution is

being discussed and erroneous to call any such solution just "cacodylic acid."

S 510 has been used against the spruce beetle in two ways—post-attack injections and lethal trap trees (see Trap Trees section). In both methods S 510 is injected into the tree through frills in the bark in the same manner (fig. 14) but the former method receives the injection after the beetles have attacked standing trees while the lethal trap trees are injected and felled well before beetle attack. In both instances, the silvicide causes short "U", "S", or "Y" shaped galleries which are void of packed frass (Frye and Wygant 1971).

Figure 14.—C. K. Lister frilling a tree prior to injection of Silvisar 510.

Chansler and Pierce (1966) initiated the first testing of S 510 against spruce beetles with a post-attack injection of S 510 and Ansar 160. They obtained an 87% reduction in the brood. Egg hatch was less and the first instar suffered the greatest mortality (Chansler and Pierce 1966). Subsequent testing yielded 94% and 100% mortality for half- and full-strength S 510 treatments respectively (Frye et al. 1977). When injected at 3 feet (.9 m) above ground in mid-July, these strengths gave satisfactory control of beetles attacking the first week of July.

The lethal trap method has progressed from a single injection of one dosage rate, to various injection times, dosages, and felling times. Initial tests yielded satisfactory mortality with full-strength treatments (Buffam and Yasinski 1971, Frye and Wygant 1971). Later tests indicated half-strength treatments are just as lethal as full-strength treatments (Buffam 1971, Buffam et al. 1973, Minnemeyer 1975, Lister et al. 1976). Injections in late September or October may be ineffective if the dosage is injected after the translocation process of the spruce has dropped sharply (Buffam et al. 1973). Quarter- and tenth-strength treatments give unsatisfactory mortality (Lister et al. 1976).

Arsenic concentrations have been determined for the phloem, needles, cones, and soil. Concentrations in the phloem are highest near the frill and relatively constant above 15 feet (4.6 m). In lesser strength treatments, mortality is unsatisfactory in the upper sections of the tree because insufficient material is translocated. Arsenic concentration in the needles is higher than in the cones while the concentration in the phloem and cones is comparable (Lister et al. 1976). Concentrations in the soil were not significantly different between pre- and postinjection samples (Lister et al. 1976). The first few inches of soil have a natural level of arsenic. There is no appreciable leaching or passage from the roots into this soil within the first year after injection. In laboratory cultures, cacodylic acid did not seriously affect forest soil microbial populations or their decomposition of organic matter (Bollen et al. 1974).

Protective Sprays

Protective sprays such as lindane, Sevimol, etc., have not been intensively studied as with other *Dendroctonus* beetles. DDT was tested in the 1940's but produced erratic results on standing trees and logs (Nagel 1960*). Preflight application of 0.5% lindane on frontalin-baited trees killed most of the attacking adults and prevented tree mortality (Dyer 1973). A later test with frontalin and 0.5% lindane resulted in 5% tree mortality but killed 44,000 attacking beetles (Dyer 1975). In both of Dyer's tests, trees were only sprayed on the lower 10 feet (3 m), so, spraying to a higher level may provide better protection.

Although protective sprays have not been as thoroughly studied against the spruce beetle, there is no reason to believe they would not be as effective against it as they are with other *Dendroctonus* species. As with other *Dendroctonus* species, their use may be restricted to the protection of high value trees.

MCH, the natural antiaggregative pheromone of the spruce beetle, prevents attacks on normally attractive host material (Rudinsky et al. 1974, Furniss et al. 1976). This compound probably reduces attractiveness rather than repels the beetles.

Pheromones

Frontalin, the principal pheromone of the southern pine beetle (*D. frontalis* Zimmerman) is a compound

of spruce beetle secondary attraction (Dyer and Chapman 1971). In Canada, it, plus alpha-pinene, beta-pinene, or 3 carene, attracts beetles better than uninfested billets (Dyer and Chapman 1971). More recently, seudenol and alpha-pinene attracted more beetles than frontalin and alpha-pinene (Furniss et al. 1976) although seudenol attracts predominantly males, while frontalin attracts 60%-70% females. However, female infested billets are more attractive than any of the frontalin-terpene combinations (Dyer and Chapman 1971). Logs with one unmated female attract more beetles than unifested logs or logs with pairs of beetles (Dyer and Taylor 1968). Frontalin on spruce trees induces attacks, and natural secondary attraction develops even though the beetles can not overcome the tree resistance (pitch) (Dyer 1975).

The spruce beetle also responds to the secondary attraction of the Douglas-fir beetle (*D. pseudotsugae* Hopkins) in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) as well as in white spruce logs (Chapman and Dyer 1969). Adults will land on the Douglas-fir logs but will not create galleries in them.

MCH (3-methyl - 2-cyclohexen - 1-one), the natural antiaggregative pheromone of the Douglas-fir beetle, represses spruce beetle attacks; reducing the attraction of spruce beetles on beetle-infested logs by 99% (Kline et al. 1974) and the number of attacks on spruce bolts (Furniss et al. 1976). MCH is released when a male enters the recently created female gallery but which sex produces the compound is unknown (Rudinsky et al. 1974). Liquid MCH deployed in glass vials along the tree trunk reduced attack densities to 0.01 per square foot (929 cm²) (Rudinsky et al. 1974). Granular MCH completely protected logs during the first two flight periods but decreased in effectiveness over time. At the end of eight weeks attacks were one-fourth as numerous as on the control trees (Rudinsky et al. 1974).

Pheromone baited standing trees for control purposes are seriously hampered by windfall (Dyer and Safranyik 1977). Windfall may so reduce the efficiency of the baited trees that 34 trees must be baited for each windfall to trap 90% of the population (Dyer and Safranyik 1977). Unless more efficient pheromones or pheromone dissemination methods are found, the effectiveness of pheromone baiting to manage spruce beetle populations over large areas is limited.

Trap trees

Trap trees are living, merchantable-sized spruce which are felled to attract infestations of the spruce beetle (Nagel et al. 1957). The main objective of the trap tree is to decoy the beetles away from living, standing trees. Once the trap tree is infested, it can be milled, burned, solarly heated, or treated chemically. Trap trees effectively attract beetles up to one-quarter mile (0.4 km); less effectively up to one-half mile (0.8 km) (Nagel et al. 1957).

In Colorado, trees felled in the fall were more attractive to the beetles than trees felled in the spring (McComb 1953), although the spring-felled trees were cut after beetle flight began. In the northern Rocky Mountains, trap trees felled in May or June prior to beetle flight were preferred over trees felled the previous September (McComb 1955). The spruce forest in Colorado commonly has considerable depths of snow in May which often precludes the felling of trap trees before beetle flight.

Trees felled in the shade sustained more attacks than those felled in the sun (Nagel et al. 1957). Unbucked trees may make better traps than bucked trees because the branches may shade the bole and also hold it above the ground to lessen the development of fungi (Wygant 1960*). Bucked trap trees, while easier to handle at a later date, have a greater chance of settling in the duff and thus precluding attacks along the bottom surface.

The trap tree method has been modified in the last few years (see Section on S 510, Frye and Wygant 1971, Buffam 1971, Buffam et al. 1973, Lister et al. 1976). Prior to felling, the trees are injected with silvicides. These arsenical compounds are translocated throughout the bole. When the tree is attacked after felling, they cause mortality to the brood. The lethal trap tree has two advantages over the traditional trap tree; the brood is killed in the tree so that further treatment is not required, and the negated postattack treatment means that trap trees can be created quite distant from a road system.

The lethal trap tree method has also been further modified in that the injected trees were not felled. These have not been as effective as the traditional traps since beetles prefer the downed material.

Resistant trees baited with frontalin are also potential traps in which reproduction is prevented and many parent adults die (Dyer and Safranyik 1977). Attacks in standing trees are induced by the frontalin, but the tree resistance (pitch) can not be overcome.

Traditional trap trees have three advantages over standing trees for absorbing beetles: beetles prefer downed material; beetles infest a greater proportion of the bole; and mean attack density is greater. The combined effect of these factors means a larger number of beetles are absorbed in the traditional trap tree.

Comparing attack densities from different studies, an 18-inch (46-cm) shaded trap may absorb 8 to 14 times as many beetles as an 18-inch (46-cm) standing tree (tables 2 and 6). In one field test, a windfall absorbed about four times the number of attacks as a baited standing tree (Dyer and Safranyik 1977).

The number of trap trees to be felled depends on the attacking beetle population and the size of the traps. Since the trap tree may absorb 10 times the number of beetles a standing tree will absorb (Wygant 1960*), the number of traps will be less than the number of infested standing trees. Nagel et al. (1957) recommended one trap for every four to five infested standing trees, while Wygant (1960*) recommended the following ratios: 1:10 for static infestations and 1:2 for increasing infestations. A more precise number to be felled may be calculated using table 6 if an estimate of the beetle population and size of the prospective traps are known.

Where the trap trees are to be felled by a logging contractor, Hester (1960*) advises the trap trees be high quality trees, located in accessible places and in groups of 50 to 100. This encourages the operator to remove the material at the proper time. When only four or five trees are felled away from haul roads, operators resist returning for them, or they may be forgotten because of their small number (Hester 1960*).

Table 6.—Number of beetles absorbed by a trap tree of specific diameter based on attack densities from McComb 1953 and Lister et al. 1976. Densities for the top and lateral sides not available in Lister et al., so they were derived from McComb's data in the same proportion as the bottom samples.

DBH	McComb 1953		Lister et al. 1976
	Sunlight	Shade	Partial Shade
6	238	586	114
7	584	1,386	268
8	720	1,770	344
9	976	2,398	464
10	1,220	2,996	580
11	1,502	3,690	714
12	1,800	4,422	856
13	2,412	5,926	1,148
14	2,678	6,580	1,274
15	3,078	7,566	1,466
16	3,474	8,538	1,654
17	3,886	9,550	1,850
18	4,326	10,630	2,058
19	4,786	11,762	2,278
20	5,312	13,054	2,528
21	5,822	14,306	2,770
22	6,352	15,610	3,024
23	6,906	16,970	3,286
24	7,480	18,382	3,560
25	8,082	19,860	3,846

Provision for trap trees and their subsequent removal may be a stipulated requirement in the timber sale agreement, since trap trees left unattended in the forest may contribute to the buildup of beetle populations. Hester (1960*) lists the following clause as one possible addition to a logging contract for spruce:

> "The purchaser will be required to fell a number of green trap trees as designated by the Forest Service. These trees will be felled after September 1 and will be left unlimbed and unbucked until the spruce beetle flight has taken place the following summer. This material will be removed by logging after August 1 the year following cutting, provided that the maximum number of trap trees required during the period of this contract shall not exceed 10% of the volume of the sale."

Frontalin baited trap trees also attract clerid beetles (Dyer 1973). This is advantageous in a suppression program because the clerids arrive before the spruce beetle and then may consume the maximum number of spruce beetles. It is a disadvantage, however, if the baited trees are treated with an insecticide because the clerids are killed along with the beetle.

Silvicultural Treatments

Alexander (1973) suggests several modifications in cutting treatments if spruce beetles are a threat. When spruce beetles are present in the stand to be cut or in adjacent stands in sufficient numbers to pose a threat, and less than the recommended percentage of basal area to be removed is in susceptible trees, Alexander suggests any attacked and all susceptible trees should be removed in the first cut. This will remove most of the larger spruce and is, therefore, a calculated gamble in above average wind risk situations. Subsequently attacked trees should be salvaged. If more than the recommended percentage of basal area to be removed is in susceptible trees, three options are available: (1) remove all the susceptible trees, (2) remove the recommended basal area in attacked and susceptible trees and accept the risk of future losses, or (3) leave the stand uncut. If the stand is left uncut, probably less than half of the residual basal area would be lost, but most of the surviving merchantable spruce would be of small diameter.

There are no precise guidelines for cutting old growth spruce and maintaining low beetle populations. Some guidelines are indirectly available from the stand rating system of Schmid and Frye

(1976). High risk stands are located on well-drained sites in creek bottoms, have an average diameter of live spruce more than 16 inches d.b.h., have a basal area of over 150 square feet per acre (14 m^2 per 0.4 ha), and a proportion of more than 65% spruce in the canopy. Since the beetle prefers older, larger diameter trees, they should be removed first while trying to lower the basal area, average diameter or percent composition of the stand. Generally maintaining these stand characteristics below the high risk level may be effective guidelines.

Guidelines for handling logging residuals are available (Schmid 1977). Trees should be cut as low to the ground as possible to reduce stump height, preferably less than 1.5 feet (0.5 m). Cull logs and tops should be limbed and the branches kept away from the bark surface of the bole. After limbing, the cull logs and tops should be positioned away from any shade and left unpiled unless they are to be burned. Their directional orientation is not important. Logs and tops should be cut into short lengths, the shorter the better. While full length logging removes the merchantable host material (Beckwith et al. 1977), complete removal or destruction of all cull logs and tops would eliminate the most significant host material left in the woods. If trees are logged full length, then the diameter of the small end should be 3 to 4 inches (7.6-10.2 cm).

Except for complete elimination of host material, even the previous recommendations will not keep beetles from inhabiting the bottom surfaces of logs and tops. If high beetle populations are subsequently found in these surfaces, they should then be treated by solar heat, with chemicals, or burned.

Where a substantial spruce beetle population exists in the adjacent forest, it may be wiser to leave the logging residuals rather than remove or destroy them immediately after cutting. Since the beetles will seek host material as they emerge, suitable residuals will attract beetles and reduce mortality of standing trees. After infestation, the residuals must be removed or treated.

These logging residual guidelines are applicable under selective, shelterwood, or clearcut silvicultural systems. The selective system offers more shade for the residuals than does a clear cut. Under a selective system, prompt removal may be the best guideline.

The guideline for windthrown trees—salvage as soon as possible, or desirable. The lone exception is the situation where removal encourages further uprooting of the edge of the stand. In some clearcut areas, trees have been windthrown along the edge. Within 1-2 years they have been removed because of the potential beetle threat, but then further windthrow occurred. Rapid removal prevented the edge trees from developing wind firmness (Alexander 1976*). In this situation, it may be better to leave the windthrown trees to the beetles even if a few adjacent standing trees are sacrificed. An intensive evaluation of the adjacent stand and the beetle population using the risk rating system of Schmid and Frye (1976) and the blowdown prediction system of Schmid (1978*) would determine whether to salvage or leave the windthrown trees.

Beetle Management Policy

Historically, control efforts usually began after an infestation had caused substantial tree mortality (hundreds of trees). Efforts emphasized sanitation cutting and chemical spraying. Few stands received preoutbreak actions designed to reduce or eliminate tree mortality (Schmid and Frye 1976). This is a questionable approach. In an economic analysis of the White River outbreak, Vaux (1954) notes that the total value of the protected spruce resource was about equal to the cost of the program. Net benefits were confined to the saved recreational values; other considerations (i.e., watershed protection, fire hazards and wildlife population changes) could not be assigned economic values. Vaux further notes that, unless the competitive disadvantage of the spruce resource changes, the value of the timber and hence the benefit-cost ratio would not change.

If forest managers are to move away from this post mortem approach — always waiting until the infestation kills hundreds of trees before initiating action — and begin to manage beetle populations, then effort must be made to reduce the potential for a beetle outbreak. Vaux suggested such a change in 1954, stating "the job of forest insect . . . control can not be appraised on a merely technical level. It must be considered as an integral part of the whole program of forest development and management." We suggest a first step in this direction would be to determine the management objectives for each spruce-fir stand, and in accord with these objectives, designate each stand as a beetle management or no management area.

Areas designated as beetle management areas could receive either silvicultural or suppressive action. The particular action prescribed for each stand would vary. Some stands might receive light thinning or harvest cuts, while other areas might receive direct and intensive suppressive actions. Areas with endemic infestations may only be surveyed periodically until the infestation warranted remedial action. The main characteristic of each stand with a beetle management classification is that the stand could, if necessary, receive either direct or indirect suppressive action.

The primary management objective in the beetle management stands may be timber production, but even good timber producing stands may have another objective with higher priority. In fact, those stands with timber production as the primary objective may be in the minority. Vaux (1954) notes that 70% of the forest land in Colorado is in public ownership. As such, it is subject to multiple use considerations, and timber production must, therefore, compete with other uses — recreation being currently a much more potentially dominant future use.

In contrast, nonmanagement stands would not receive silvicultural or suppressive actions. Beetle populations would be allowed to increase and subside at their natural rate. They may decimate the spruce in a particular stand(s) but this does not mean the area or the beetles would be totally ignored. On the contrary, the population might be periodically evaluated since it could always disperse into an adjacent and possibly beetle management area and cause undesirable tree mortality. The most obvious example of nonmanagement areas is wilderness, although natural areas, National Parks, experimental forests and private land may also be included.

A further and simultaneous step in the spruce beetle management area would be to rate each stand into a potential outbreak category using the system of Schmid and Frye (1976). This would benefit the forest manager by: (1) identifying the stands most likely to have outbreaks, and (2) providing the impetus for active involvement in a neglected aspect of beetle management: modifying stand conditions. The manager could direct his silvicultural activities into stands with the highest outbreak potential.

The promotion of preoutbreak silvicultural practices and stand ratings does not mean that suppressive activities should be abandoned. Some areas may need suppression programs because: (1) silvicultural activities can only proceed at a certain rate, so that years will pass before all of the beetle management stands receiving silvicultural treatment will be in a low potential outbreak status, and (2) suppressive action may be the best short-term measure. The State of Colorado has about 3.4 million acres (1.4 million ha) of spruce-fir sawtimber on commercial forests (Alexander 1974), most of which is old-growth and 75% of which is in either roadless or reserved categories (Cahill 1976*). Although large areas of old-growth forests are being converted to timber producing stands that must be managed (Alexander et al. 1975), the rate of conversion is less than 0.5% per year. At this rate, it will take more than 100 years to convert the old-growth, and thus, substantial acreages of old-growth will continue to exist for at least 50 years.

Suppression measures will be needed for the short-term because silvicultural activities will not proceed fast enough. They will also be needed for the long-term because (1) some stands, even though designated as beetle management areas, will not receive silvicultural treatment because their primary management objective will be something other than timber production, and (2) measures must be available to handle instances when beetles in nonmanagement areas are a threat to a managed area. Whenever possible, suppression measures should be linked to a silvicultual treatment so that the stand conditions contributing to the infestation are modified and the inevitable is not just temporarily postponed.

Some will question the effectiveness of suppression programs as well as these proposed approaches to beetle management. Suppression methods can always stand improvement, but ineffectiveness is generally the result of an incomplete job. Chemicals, for example, will satisfactorily suppress populations in cull logs, but only if the logs are sprayed completely. If not enough trap trees are felled to absorb the emerging beetles, standing trees will be infested. Or an outbreak may become so large that the suppression program is inadequate. The program manager may then treat the most accessible or least costly trees in order to maintain the lowest possible treatment cost per tree. This action frequently expands the treatment program to a large area rather than confining it to a particular drainage. As a result, the percentage of untreated trees in a specific drainage may be high so the outbreak continues. Actually, suppression in the properly treated trees was satisfactory, but since so many trees remained untreated, the treatment appears ineffective. Obviously these situations must be eliminated and the undesirable side effects of such programs minimized. Otherwise, the public, through law or departmental edict, will restrict our options which may seriously handicap suppression efforts.

In summary, we have enough knowledge of the beetle and suppression techniques to prevent large infestations if we desire. Basic to the development of a control strategy is a need to know the objectives for the particular stand(s). If the objectives are known, then we can begin to integrate beetle management into forest management.

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This report summarizes the literature on the spruce beetle in the western United States, primarily in the Rocky Mountains. Information is presented on life history and behavior, host relationships, mortality agents and impacts of infestations. A section of suppression details the current status of chemicals, pheromones, trap trees and silvicultural treatments. The initial steps in managing spruce beetle populations are stated in the final section on beetle management policy.

Keywords: *Dendroctonus rufipennis,* spruce beetle, bark beetle.

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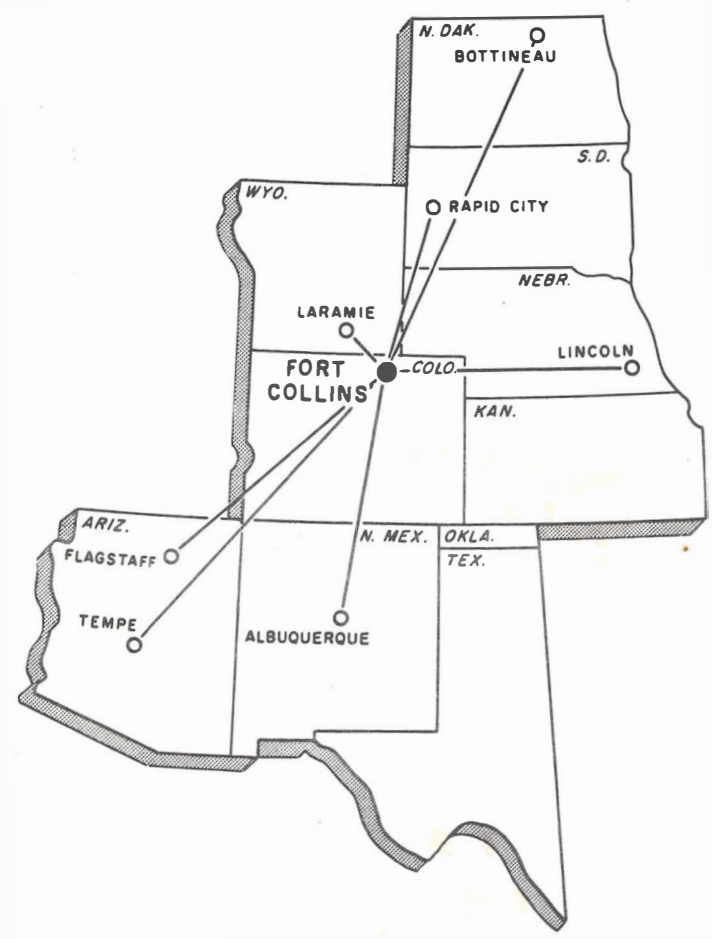
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